

NEW STUDIES
OF
TROPICAL AMERICAN
BIRDS

ALEXANDER F. SKUTCH

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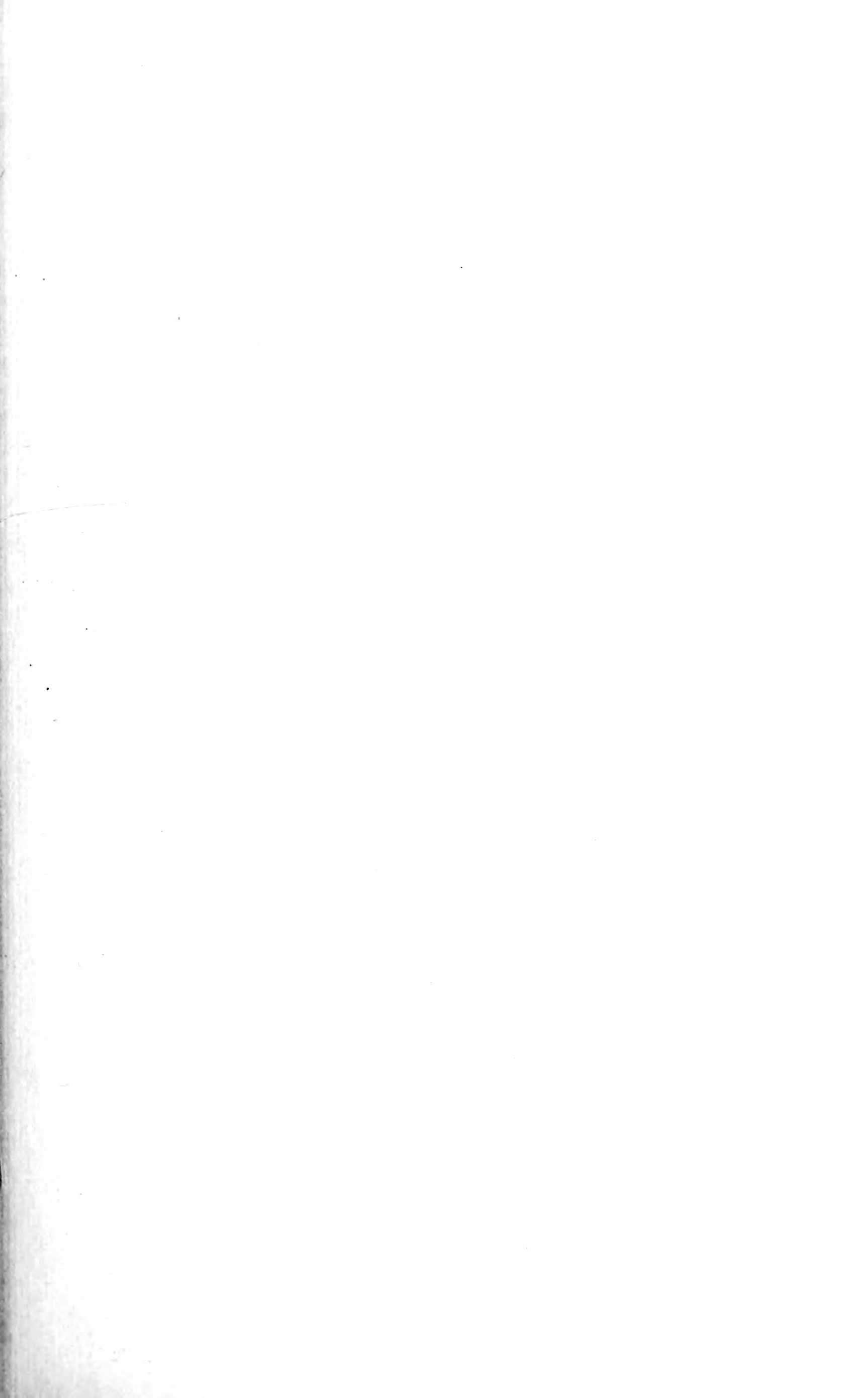
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NEW STUDIES
OF
TROPICAL AMERICAN
BIRDS

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, NO. 19

Editor, Raymond A. Paynter, Jr.

NEW STUDIES OF TROPICAL AMERICAN BIRDS

ALEXANDER F. SKUTCH

ILLUSTRATIONS BY DANA GARDNER

To
David W. Snow
and
Barbara K. Snow
who have contributed
greatly to our knowledge
of tropical American birds

CAMBRIDGE, MASSACHUSETTS

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1981

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PREFACE

Five of the life histories in this book are of birds about which I have not previously published. Those of the elusive Rufous-winged Woodpecker (*Piculus simplex*) and Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) are based largely upon single nests that I had the good fortune to follow in detail from building to their successful conclusion. Because of loss of nests difficult to find, the accounts of the Fork-tailed Woodnymph (*Thalurania furcata*), Greenish Elaenia (*Myiopagis viridicata*), and Southern Beardless Flycatcher (*Camptostoma obsoletum*) are less complete, but they add significantly to information published by others, upon which I have drawn to supplement my own observations.

The other 22 species treated in this book are birds whose life histories I have already published. Since writing these earlier accounts, in one instance nearly 50 years ago, I have continued to live among these birds and have learned so much more about them that new reports appear to be desirable. In preparing these updated life histories, I have condensed material already published in order to give the most comprehensive accounts of these species that available information permits. I have taken this course because some of these earlier life histories are in a book (Skutch, 1954) that has long been out of print and difficult to obtain, while others are scattered through journals, often dating many years back, which are readily consulted only in well-stocked ornithological libraries. Accordingly, the present book contains much new information, while it makes older information readily available to the growing number of people, amateurs as well as professionals, interested in the birds of tropical America.

Unless otherwise stated, the studies in this book were made at "Los Cusingos," which has been my home since 1941. This property of about 100 ha stretches along the right, or western, bank of the Río Peñas Blancas, which arises in the Cordillera de Talamanca and delivers its water, through the Río General, to the Río Térraba, the major river on the Pacific slope of southern Costa Rica. The farm lies just below the hamlet of Quizarrá, at an altitude of about 750 m. It contains, in addition to planted fields and much resting land in various stages of natural reforestation, a large tract of old rain forest, one of the few that remain in the Valley of El General. Detailed descriptions of the valley and the farm, as I knew them four decades ago and as they are today, may be found in my books, *A Naturalist in Costa Rica* (1971) and *A Naturalist on a Tropical Farm* (1980).

Dana Gardner generously drew the figures for this volume. Their publication was subsidized by Mr. Willard L. Gardner, Mr. and Mrs. Henry Guthrie, Mrs. Alvina Hayman, and the Western Foundation of Vertebrate Zoology. I am grateful to them, and to my wife, Pamela, whose faithful attention

PREFACE

over the years to the details of daily living has enabled me to devote much time to these studies.

ALEXANDER F. SKUTCH

Finca "Los Cusingos"
San Isidro de El General
Costa Rica
31 August 1979





FIG. 1. Blue Ground-Dove, *Claravis pretiosa*.

Family COLUMBIDAE
WHITE-FRONTED DOVE

Leptotila verreauxi

Big enough to be called a pigeon, the White-fronted, or White-tipped, Dove is plainly attired. Its upper plumage, including wings and tail, is grayish brown, paling to pinkish brown on the crown and almost white on the forehead. The underparts are lighter, whitish on the throat, more grayish on the breast and sides, white on the abdomen and undertail coverts. The outer tail feathers are black subterminally, with broad white tips prominent as the bird takes wing. The brightest color is the cinnamon lining of the wings, conspicuous when they are raised, but not sufficient for identification, as this color is shared with other members of the genus. The purple to green iridescence on the hindneck, which is mentioned in descriptions and depicted in certain paintings of this dove, escapes notice in the field. The bill is blackish, the legs and toes dull red with black toenails. The bright yellow to orange eye is surrounded by bare blue skin, which extends in a narrow streak to the base of the bill. The yellow eye of the Gray-chested Dove (*Leptotila cassinii*) is set amid red rather than blue skin, and this is perhaps the most certain way to distinguish these two rather similar doves.

The White-fronted Dove has a wide geographic range, from southern Texas to western Peru, Brazil, central Argentina, Trinidad and Tobago. Its altitudinal range is also great, from sea level up to 2,400 m in Mexico (Friedmann *et al.*, 1950), 2,600 m in Guatemala (my records), and nearly 3,050 m in northern Venezuela (de Schauensee and Phelps, 1978). In intermediate regions it has not been found so high: to about 1,825 m in Honduras and western Panama (Monroe, 1968; Wetmore, 1968), while in Costa Rica I have not seen it above 1,525 m. A bird of light woods and semi-open country rather than the rain forests, this dove is abundant over the whole Pacific slope of Central America, but on the Caribbean side its presence is more restricted. Here it is found chiefly in the drier parts of interior valleys, such as those of the Río Motagua in Guatemala and the Río Ulua in Honduras. Apparently it is increasing on the Caribbean littoral as the rain forest is cleared, as it certainly has on the southern half of the Pacific slope of Costa Rica, where rain forests hardly inferior to those of the Caribbean region have been largely replaced by farms.

Although we read in Bent (1932) that, in the lower valley of the Rio Grande of Texas, White-fronted Doves, migratory here at the northern limit of their range, inhabit dense forest and perch on the highest treetops, this is far from true of the resident races that I know in Central America and northern South America. In these regions the dove avoids both the interior of heavy forest and broad open fields, and it rarely, in my experience, perches much above 7–9 m. Among its habitats are shady gardens and plantations, including those of coffee and bananas, bushy pastures intersected

WHITE-FRONTED DOVE

by a maze of cowpaths, thickets, and light, open woods. In the more arid parts of its range, where Inca (*Scardafella inca*) and White-winged (*Zenaida asiatica*) Doves abound amid cacti and thorny scrub, it prefers the lush vegetation of the river bottoms and other low ground. Although in the rainy Valley of El General, White-fronted Doves mingle extensively with the rufous-naped race of the Gray-chested Dove (*L.c. rufinucha*), the latter is often seen amid the heavier vegetation, such as the margins of the rain forest, that the White-fronted Doves avoid. I have never seen these doves in flocks.

FOOD

As far as I have seen, the White-fronted Dove forages wholly on the ground, walking with bobbing head, picking up small objects that are apparently seeds and berries. It eagerly seeks maize and enters open granaries to gather loose grain, but I have not known it to attack standing crops. At daybreak, when we feed the chickens on the lawn, several White-fronted and Gray-chested Doves, sometimes six or eight, are nearly always present to share the corn. They have not learned that the grains that I throw toward them are harmless missiles, and always retreat as they fall, to reappear from behind the shrubbery after a short interval. They do not disdain spoiled grain that the pampered chickens leave untouched. Sometimes White-fronted Doves chase Gray-chested Doves, as they do to others of their own kind; but I have not seen a fight, and both species share the food. That rivalry between the related species is not serious is also attested by the fact that I once found their occupied nests about 9 m apart, on opposite sides of a path through low second-growth.

VOICE

In December when, after long months of heavy rain, reduced precipitation and increased sunshine prelude the arrival of the dry season, the abundant White-fronted Doves begin their sonorous calling. They are most vocal in the warmer parts of the day, toward noon and in the early afternoon. Perching inconspicuously amid concealing foliage, often of an orange tree, they repeat deep notes over and over. Puffing out his chest but keeping his bill closed, the dove emits a moaning *coo-ooo* in a peculiar tone that makes it unmistakable. Utterances more rarely heard are a *coo-woo* and *cu cu cu coo-ruuu* that are higher in pitch and more musical, almost soprano in tone. A dove sometimes produces these different calls alternately. The utterances of the Gray-chested Dove and Ruddy Quail-Dove (*Geotrygon montana*) are easily mistaken for that of the White-fronted Dove but sound more mournful. Although White-fronted Doves are most vocal in the dry season, when chiefly they nest, in some years they call much from July to November in their minor breeding season. Amid the coffee groves and low copses of the central highlands of Costa Rica, I have heard the deep, hollow call in October when these doves are mostly silent in the wetter

WHITE-FRONTED DOVE

region of El General. Over much of the Pacific slope of Central America this is one of the characteristic bird sounds through much of the year.

NESTING

Nesting begins sparingly in December and reaches its peak in March. Most of the 26 nests that I have found here were a meter or two above the ground, in low, dense thickets, tangles of vines, or weedy fields. The lowest of all the nests I have seen was only 30 cm up on matted calinguero grass (*Melinis minutiflora*) on a steep slope, above the edge of a thicket. Two nests rested on stout plants of the orchid *Oncidium* growing on trees. Four nests were on stumps and in thick crotches, from 1–5 m up. The unusually high nests at 5 m were built in consecutive years in the main fork of a large burío tree (*Heliocarpus appendiculatus*) in our garden. Here was a platformlike expanse, shaded by a small epiphytic shrub, between four thick upright branches. The highest of all the nests that I have seen was 6 m up amid the dense foliage of an orange tree in a pasture. Of the 23 nests whose height I have recorded, two were below 1 m, 13 between 1 and 2 m, and eight at greater heights, with the extreme range 3 to 6 m. Wetmore (1968) occasionally found nests on the ground in Panama.

I watched building at two nests where one member of the pair was distinguished by abnormal plumage. In each case the dove that later incubated through the night, indicating that she was the female, sat on the growing nest to arrange materials that her mate brought to her. He gathered straws and twiglets from the ground, shook them to test their soundness, and, if they were satisfactory, carried them up to the nest, always one at a time, as far as I could see. Usually the male stood on his mate's back while he laid the contribution beside her, but sometimes he passed by her. Often she rapidly vibrated the tips of her wings as he approached. He never arranged what he brought, leaving this wholly to the female. After he flew down for more material, she shaped the nest, rotating to tuck in pieces all around. The pieces that he brought became smaller and finer as building proceeded. If the male delayed supplying materials while the female sat on the nest, she called softly. One male brought 12 pieces from 8:20 to 9:20 and 14 pieces in the following 33 minutes. From 8:51 to 9:48 next morning he came with material 10 times. After a spell of building the female sometimes joined her mate on the ground, where they touched bills and nibbled one another's neck feathers. This nest was completed in three or four days.

White-fronted Dove's constructions are among the more substantial of pigeons' nests. A solidly made nest was a thick, shallowly concave platform 13 to 15 cm in diameter, not including the projecting ends of sticks, and about 9 cm high. Among the 350 pieces (not including the finest fragments) were weed stems, straws, sticks, dry pieces of vines, fragments of fronds of the bracken fern (*Pteridium*), rootlets, and the like. The longest stiff pieces were two crooked straws about 30 cm long; but three very thin,

WHITE-FRONTED DOVE

curved pieces of vine were, when straightened, 50, 46, and 40 cm long. Most pieces were under 25 cm long. This nest weighed 68 grams and contrasted with the much slighter nest of a pair of rufous-naped Gray-chested Doves about 9 m away.

Another White-fronted Dove's nest measured 15 by 7.5 cm, weighed 36 grams, and contained 109 pieces. These materials were mostly coarse and included dry grasses and weed stems, many with roots attached, long dying fern fronds, and twiglets. Among the longest pieces were very slender vines 71 and 61 cm long, grass stems 50 and 46 cm, and slender fern fronds up to 48 cm. Many of the pieces were branched. They were well interlaced into a firm, coherent structure that could be removed intact from its site in an orange tree. One nest was made chiefly of pieces of the grass and bracken fern amid which it was situated. A nest built upon an orchid plant above a privet hedge was a slightly concave platform, composed almost wholly of slender, stiff, leafless twigs trimmed from the hedge. Some were 30 cm or more long and projected far beyond the body of the nest. Occasionally White-fronted Doves lay their eggs on a frail, shallow structure.

Of 24 nests, 20 contained two eggs or nestlings; four, a single egg or nestling. From two of the latter an egg or nestling might have been lost; but another two of these nests, for second and third broods, were followed carefully during the period of laying and almost certainly never received second eggs.

To learn the exact hour of laying is difficult because the doves spend so much time on the nest on the days when they lay, and too frequent disturbance might cause loss of an egg or desertion of the nest. When one female settled on her nest in the evening of 31 March it was eggless. She sat through the night and by 7:00 next morning had laid her first egg, which was covered intermittently through the day of 1 April. At 7:10 on 2 April there was still the single egg. On frequent visits from 8:00 to 15:00 that day I always found a dove on the nest and did not disturb it. Finally, at 15:00 I put the dove off and found two eggs, the second of which had been laid since 7:10 that morning. At two other nests the second egg was laid between 7:00 and 10:30 on the day after I found the first egg, and at another nest it was laid before 9:30. In two-egg nests I have never failed to find the second egg on the day after I first saw the first egg, although I did not always know when this first egg was laid. These observations indicate that the first egg is laid either in the evening, during the night, or, more probably, early the next morning, and the second egg is laid more than 24 hours, but considerably less than 48 hours, after the first.

Between seven and ten days after she lost her eggs, a female, recognizable by abnormal feathering, laid the first egg of a replacement set, 33 m from the site of her first nest. In the following year this same female again lost her first set and laid the first egg of her replacement set 44 days later. Her two nests were in the same two sites as in the preceding year,

WHITE-FRONTED DOVE

but she could have nested elsewhere in this long interval. Two broods are sometimes raised, as told beyond.

The eggs are white or sometimes pale buff, without much gloss. The measurements of 15 eggs average 29.6 by 21.6 mm. Those showing the four extremes measured 31.0 by 21.0, 29.4 by 23.0, 27.8 by 21.8, and 29.4 by 20.2 mm. This does not include a runt egg which was only 22.2 by 16.7 mm.

In 26 nests in the Valley of El General, 600–900 m above sea level, eggs were laid as follows: December, 1; January, 1; February, 4; March, 8; April, 4; July, 3; August, 2; September, 2; October, 1. In May and June, when the great majority of the small birds of the valley breed most freely, no White-fronted Doves' nests have been found, although in these months I have searched for birds' nests most diligently. A similar discontinuity in breeding occurs in rufous-naped Gray-chested Doves and Blue Ground-Doves (*Claravis pretiosa*) in the same region. Some individuals nest in both the early and the late seasons. In other regions, even at about the same latitude, White-fronted Doves appear to breed continuously rather than in two separate seasons. Of 59 nests recorded in Trinidad, where the species nests throughout the year, 41 were found between March and July (French, 1973).

Incubation follows the widespread "pigeon pattern," with the eggs continuously covered in two long sessions every 24 hours. Although the sexes of White-fronted Doves are alike in appearance, I have no reason to suppose that in their incubation habits the species differs from other pigeons in which the sexes are readily distinguished, and in which the female takes the night session and the male sits through much of the day. The incubation period, as determined at three nests, is approximately 14 days. Hatchlings bristle with the straw-colored, hairlike feather tips typical of newborn pigeons. When they are nine or 10 days old, their feathers expand, producing a plumage much like that of the adults, except that it is duller and the feathers of the back and breast have pale margins, giving a scalelike appearance. The juveniles' outer retrices have white tips, as in the adults. The nestling period was 15 days at one nest, 16 days at two nests, and 18 days for a lone nestling that suffered certain mishaps, as will presently be told. Fledglings, which leave the nest after 16 days, can fly and walk competently. More details of incubation and parental care are given in the following section.

Like other species of *Leptotila*, White-fronted Doves are among the most devoted of avian parents. They keep their nests scrupulously clean. While covering eggs or nestlings they permit themselves almost to be touched by human hands. Even after the young are well feathered a parent is to be found on the nest with them much or most of the time, sometimes sitting with a nestling on either side. They may try to defend their nest by striking an approaching object, such as a mirror raised to it, with a wing. When finally driven from the nest they give prolonged distraction displays, acting as though they were seriously injured and could not fly.

WHITE-FRONTED DOVE

Their presence on the nest long after the young need brooding in fair weather, in conjunction with these displays, may often save the young doves from predators. As I have seen at several nests, while the parent flutters and limps off in one direction, the fledglings fly off in another direction. The behavior of injury-feigning White-fronted Doves supports my belief that birds are never in fuller control of all their faculties, nor act with greater precision, than when they lure intruders from their nests or chicks by behaving as though they were incapacitated or having a fit. Elsewhere I have described White-fronted Doves' distraction displays in detail (Skutch, 1964, 1976).

I witnessed an impressive display of parental devotion and courage by the female of a pair that built a low nest just within the dense stand of scrambling *Dicranopteria* fern behind our house. The more timid male would fly from the nestlings if I peered into the fern where he brooded, but his mate permitted herself to be lightly touched before she flew off, without displaying. One evening in the twilight, I heard a repeated loud sound from the fern, as though the brooding female were striking something with a wing. I could see little amid the shadows of the fern, so I ran into the house for a flashlight. As I returned a minute or two later, the thuds continued. The beam of light revealed part of a fairly large snake close to the nest. I struck at it with a stick, but the wiry fern stipes broke the force of the blow, and the snake vanished into the tangled mass of fern. Although this encounter shook the nest, the dove remained sitting. Next morning only one nestling was present. Whether the snake swallowed the other, or it was knocked from the nest during the conflict, I could not tell; it was not on the ground below. Three evenings later, I again heard wing-flapping in the twilight, less loud than the slapping sound of the earlier occasion. I went repeatedly to investigate, but saw no snake. Later in the night, I found the dove sitting peacefully on her nest, apparently covering her remaining nestling. By morning, the nest was empty.

SECOND BROOD

Juveniles of the first brood.—While I fed my mare on the evening of 10 March 1979, a White-fronted Dove flew past and disappeared into the dense foliage of a nearby orange tree. After nightfall search with a flashlight disclosed four doves roosting on a slender branch of this tree, about 4.5 m up. Three were in close contact, the fourth about 5 cm away from the trio. All faced in the same direction, with their heads exposed, as I have always found doves sleeping, rather than turned back to nestle among the feathers of a shoulder. On the following night the doves roosted two by two on the arms of a forked branch. The members of each couple were in close contact and faced the same way. All four doves were well grown, but one member of each pair was slightly shorter than the other. Evidently they were parents with young. One of the parents, which I had seen walking

WHITE-FRONTED DOVE

in the garden or eating the chickens' corn, had an exceptionally dark head and throat.

On the following nights these doves continued to roost in the orange tree, arranging themselves in various ways. After nightfall on 13 March I could find only three, pressed close together in a row, the two end doves facing in the same direction and the middle dove in the opposite direction. The following night all four were again present, with two roosting in contact and one a few centimeters from each side of the pair. On 15 March only three were visible, all resting in contact. On the next night only two were present, pressed close together, but on 17 March the two were about a meter apart.

Building.—On the morning of 18 March I found the parents building a nest, already well advanced, in the orange tree where they roosted. Six meters up on a horizontal branch well screened by foliage, it was a meter higher than any other White-fronted Doves' nest that I have seen. While the normally colored adult sat on the nest arranging materials, the dark-throated dove gathered straws from the ground, carried them up, and laid them beside her, thereby revealing that he was the male. The two young doves were nearby and presently one came to the nest and begged for food from the female. Thereupon, she flew beyond view with her mate. For several minutes the young dove remained on the nest, moving around, preening, and fiddling with the materials. Then the other young dove joined the first on the nest. They stayed there together for a few minutes, then the first left. For the next hour the second sat on the nest, at intervals preening or touching the materials with its bill. This whole time the first young dove perched quietly nearby, except for another brief interval when it joined its sibling on the nest.

Laying and incubation.—On the following day, 19 March, between 7:30 and 17:00, an egg was laid. A parent was so constantly on the nest that I could not time the laying more exactly without disturbing it. As the day ended a young dove sat on the nest with its breast over its mother; but I did not find it there after nightfall. A juvenile roosted alone high in the orange tree. No egg was laid the following day or thereafter; this second-brood nest did not receive the usual two eggs. Again that night the two young doves roosted in close contact on the branch where I first found the family sleeping. Late on the rainy afternoon of 21 March the female and a juvenile sat side by side on the nest, as though both were incubating the single egg. There they stayed until it was quite dark, while the other young dove slept alone high in the orange tree. By day the two young kept close company, walking over the lawn and pasture together. For a few nights more a single juvenile slept in the orange tree. After 26 March I no longer found either of them in the tree where their parents continued to attend their egg; and soon I could not distinguish them from the many other White-fronted Doves in the vicinity. The continued close association of juveniles and parents during the early stages of the second nesting was unique in my experience with free pigeons, although Goodwin

WHITE-FRONTED DOVE

(1947) recorded an intimate relationship between a young domestic pigeon and its mateless mother, which was incubating a later set of eggs.

To learn the pattern of incubation I inspected the nest frequently, as I could do without disturbing the doves, and I watched several changeovers. Except on the last two days of incubation this pair followed the usual "pigeon pattern," with the male taking one long session each day, the female sitting all the rest of the time. The male arrived between 9:00 and 12:00, on most days between 10:00 and 11:00, and sat for four to six hours until the female returned between 15:00 and 16:00. (At an earlier nest the female returned between 15:20 and 16:33 on three afternoons.) On the ninth day of incubation, when I watched both changeovers, the male came at 10:36 and sat until his mate relieved him at 15:47, or for five hours and 11 minutes. On the last two days of incubation the male, evidently anticipating the nestlings, came unusually early; I found him there at 8:35 on 1 April and 7:10 on 2 April. Later on both mornings the female was again covering the eggs, but around 11:00 the male returned to incubate until late in the afternoon. Thus, on these two days there were four changeovers instead of two.

All changeovers were silent and unceremonious. The oncoming partner usually approached over the ground and flew up into the orange tree, to alight some distance from the nest, then waited until the sitting dove left. After reaching the supporting branch the newcomer walked along it to the nest; it never flew directly to the nest. In the morning the female left promptly when her mate arrived, but in the afternoon she might wait in the orange tree for as much as 10 or 15 minutes, until he departed, and then she proceeded to the nest.

Hatching.—At 16:37 on 2 April the incubating male started to call in a low voice. When, a minute later, the female flew into the orange tree, he picked up part of an empty shell and flew away with it. Advancing to the nest she lowered her head into it and appeared to taste or swallow something. I put her off and, raising a mirror attached to a long pole, saw a nestling lying beside half of a shell. The female soon returned to the nest but did not remove the remaining part of the shell. When the male arrived next morning his first act was to carry it away.

The incubation period of this single egg was 14 days 1 hour \pm 8 hours. Two earlier determinations of the incubation period, at nests with two eggs, were 14 days 12.5 hours \pm 10.5 hours, and 14 days 1 hour \pm 9 hours.

Brooding.—As already told, as the date of hatching approached the male came earlier to begin his session of incubation. After the nestling hatched he continued to arrive early to brood, often between 7:00 and 8:00, and, when the nestling was 16 days old, at 6:20. His sessions on the nest were now substantially longer than while he incubated, often between 6.5 and 7 hours. This young dove remained in the nest exceptionally long, and on the last three full days, when it was 15 to 17 days old, the parents' schedule of attendance changed greatly. Now, instead of taking a single turn on the nest the male took two. The female, which had been relieved

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early in the morning, returned early in the afternoon for another spell of brooding, or at least guarding, the nestling. On 17 April the afternoon session lasted from 14:09 to 16:21 when the male returned. He remained until 17:07 when his mate came to stay for the night.

On long-continued watches and frequent inspections I did not find the nestling alone until it was 17 days old, when its father, after feeding it in the morning, left it unattended for 38 minutes. The young dove was very active the last morning on the nest. The female, departing from her previous behavior, left 39 minutes before her mate's arrival at 6:29. He accompanied the nestling most, if not all, of the time until its departure in mid-morning. During its last week in the nest the nestling was so well feathered that it did not seem to need brooding, especially on fair mornings. Much of the time it sat with its head projecting from its parent's breast feathers, or even lying exposed in front of the parent; but when the afternoon deluges came it retired beneath the sheltering adult, as it did at nightfall.

Feeding.—As in other pigeons the number of meals and the total time devoted to feeding decreased as the nestling grew older. Since I could not watch the nest through my binocular and look at my watch at the same time, I could not time feeding to the nearest second and my results are only approximate. On the day after the nestling hatched the female regurgitated to it twice, for about one and then three minutes, before her departure. Although the male replaced her at 8:49, he did not start to feed until 10:12. In the next two hours he fed nine times. His spells of regurgitation, not always continuous, lasted from less than one minute to about five minutes. After midday neither parent fed the nestling. On this day it was fed 11 times, for a total of about 21 minutes. When the nestling was seven days old it was fed twice by the male and once by the female, for a total of seven minutes. When it was 15 days old its mother fed it twice and its father thrice; the time devoted to feeding was less than five minutes.

Without much doubt, food was transferred from parent to young in an increasingly copious stream as the nestling grew, and the time devoted to feeding at various ages is no indication of the quantity of nourishment delivered. Regurgitation, especially at the later stages, was a strenuous performance, the parent bringing up food with a violent, convulsive jerking of its neck and head. The head of the nestling, whose bill was inserted into the side of the parent's mouth, bobbed up and down with that of the feeder, and its wings flapped widely. The parents were inconsistent in delivering meals. One morning the female might feed the nestling before she left, while on the next morning she did not. Similarly, after returning for the night she might feed or neglect to feed.

Sanitation.—The parents cleaned the nest by eating droppings. Sometimes they did this shortly before feeding the nestling, raising the question, noticed also in other pigeons, of how they avoided returning wastes to it, if they actually did avoid this. While she brooded in the rain the female repeatedly drank rain drops from surrounding foliage.

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Nestling's development and behavior.—This nestling had two mishaps that would have cost its life but for our timely aid. Puzzled by the continued absence of the parents from the nest after the middle of the morning of 13 April, I began to investigate and soon found the 11-day-old nestling beneath the orange tree, where it had been for about three hours. Fairly well feathered, it appeared uninjured but could not fly. Whether it had been frightened from the nest or fell accidentally, I could not tell. With a long ladder it was replaced, and was brooded by its mother.

As day dawned on 16 April I failed to see the female dove on the nest. Soon she arrived and sat, but was restless and called. After seven minutes she left the nest but continued to call in the orange tree. After another five minutes she flew to the ground and walked away. An hour later I found the young dove on a pile of fallen branches at the edge of a dense thicket of the fern *Dicranopteris*. Soon it moved into the fern. Its father arrived and found it, then its mother came. They billed each other, then the male nibbled the plumage of his mate's head. She approached the nestling, which tried to push beneath her. She tried to brood it but could not make herself comfortable on the rough sticks and fern and soon abandoned the attempt. Although the 14-day-old dove was well clothed with plumage and had expanded remiges, it could fly only a few centimeters. When I caught it amid the fern it struggled mildly but was silent. Evidently parent and nestling had fled the nest during some nocturnal alarm. Replaced in the nest, the young dove was soon fed and brooded by its mother, which repeatedly billed its head while it lay in front of her.

The dark grayish brown head of the feathered nestling was marked with broad, pale gray superciliary stripes and a white crescent below each eye, which adults lack. Its eyes were brown instead of yellow, and the bare skin around them was very dull bluish instead of bright blue. From time to time it preened, sometimes while the parent beside it was preening itself too. At intervals during its last few days in the nest it took vigorous wing exercises, sometimes flapping its wings in the guardian parent's face. In the brief interval between one parent's departure and the other's arrival, the nestling was often very active, moving around, preening, stretching its wings both together above its back and flapping them, as though enjoying its freedom to exercise without a larger body looming above it.

While alone on the morning of 19 April the nestling was restless. Rising in the nest it made intention movements of flight, bowing forward and raising its tail. Early on the following morning it was active, but by 9:00 it sat quietly beside its father, revealing no inclination to leave the nest. Returning after a short absence, I found the nest empty; parent and fledgling had vanished. Later that morning I discovered the 18-day-old dove walking over the ground near the nest tree. When approached it flew very well. Possibly because its two falls from the nest had delayed development, this young dove had remained there two days longer than other White-fronted Doves.

On the evening after its first flight the young dove roosted with a parent,

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apparently the female, in the orange tree where it was raised. The two perched in contact, facing in opposite directions, about 5 m above the ground, on a branch well screened by foliage above but fully exposed below. On the following night I could find no member of the family; but on the next night, the third after the fledgling left the nest, it slept with its parent in the same place, the two pressed together and facing the same way. Thereafter these doves roosted where I could not find them.

Behavior of the parents.—While raising their nestling the parents often foraged over the close-cropped pasture around the nest tree. Often, however, they went more widely, for once I saw the male in the banana plantation, about 300 m from the nest and separated from the pasture by a belt of tall woods. When two rufous-naped Gray-chested Doves walked by the nest tree, the male White-fronted Dove chased them mildly. Otherwise I noticed no territorial defense. One evening while the female stood on the grass before flying up to the nest, an agouti (*Dasyprocta punctata*) walked close by her. Neither paid any attention to the other. Birds in their natural environments appear to know very well which of the native animals are dangerous and which are harmless.

After the young dove's departure on 20 April, nearly four months elapsed before I again noticed nesting activity. On 11 August I found a nest, already nearly finished, 3 m up in an orange tree, 8 m from the preceding nest. The male gathering material for the new nest was normally colored. If this was the same individual that had helped to raise the single nestling, he had, in the long interval, lost the abnormally dark feathers of his head and neck by molting. I am confident, however, that at least the female was the same. Again, she laid one of the rare one-egg clutches, between 9:00 and 14:05 on 12 August. Incubation began and, when I raised a mirror to the nest, the dove which had been sitting gave an excellent distraction display, limping over the ground for many yards with loosely flapping wings. Inexplicably, the nest was abandoned a few days later. Thus this pair, or one of its members, nested again in the minor breeding season after successfully raising two broods in the main breeding season early in the year.

SUMMARY

Over an immense area, White-fronted Doves range from sea level to high in the mountains, reaching 2,600 m in Guatemala and nearly 3,050 m in Venezuela. Avoiding tropical rain forest, they inhabit light woods, thickets, plantations, gardens, and shady or bushy pastures. They forage wholly on the ground and are fond of maize.

Their call, heard chiefly in the dry season, is a deep, moaning *coo-ooo*. A variant sounds like *coo-woo*.

Nests are built in thickets, vine tangles, and weedy fields, sometimes in trees. Most are from 1 to 2 m up, but rarely they are placed on the ground or as high as 6 m. To build the female sits on the nest arranging what

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her mate brings to her from the ground, one piece at a time.

The set nearly always consists of two white eggs, the second of which is laid between 7:00 and 10:30 on the day after the first appears. In the interval between layings the first egg is covered much of the time.

In the Valley of El General the main breeding season begins in December, peaks in March, and continues into April. No nest has been found in May and June; but a second, minor, breeding season extends from July to October.

The male incubates in one session of from four to six hours each day, and the female occupies the nest all the rest of the time. The two daily changeovers are silent and without ceremony. The incubation period is 14 days.

Nestlings are brooded, or at least guarded, most of the time until they fly. Through most of the nestling period the same pattern of attendance as while incubating is followed, except that at one nest the male came earlier and stayed longer. During the last two days at this nest the parents brooded with four rather than two changeovers daily.

The number of feedings, and the total time devoted to regurgitation by the two parents each day, drops sharply as the nestlings grow older.

The parents keep the nest scrupulously clean by swallowing droppings.

The nestling period is usually 16 days, but a nestling which twice fell from the nest before it could fly remained for 18 days. Sixteen-day-old fledglings fly and walk well.

Parents give prolonged distraction displays. While they lure the interloper in one direction the young fly off in another direction.

Juveniles were closely associated with their parents during the early stages of a second nesting. They roosted with their parents, often in contact with them. The young doves spent much time on the nest their parents were building, and one passed the night beside its incubating mother. Four months later these parents nested for the third time in one year.

White-fronted Doves are only mildly antagonistic to congeneric rufous-naped Gray-chested Doves. The two occupy the same areas, feed together, and have nested only 10 m apart.

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Claravis pretiosa

One of the loveliest of New World pigeons, the Blue Ground-Dove is especially attractive to students of behavior because the sexes are so strikingly different that it is easy to learn their roles at the nest. The male is largely grayish blue, with deeper blue wings spotted and barred with black. The female is buffy brown, with warm cinnamon-brown or russet central tail feathers and chestnut instead of black markings on her wings. Over its vast range from northeastern Mexico to northern Argentina and from western Ecuador to Trinidad and eastern Brazil, the species shows surprisingly little geographical variation. In southern Costa Rica I have found it from the

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Pacific lowlands up to about 1,200 m in the Cañas Gordas-San Vito region near the Panamanian border, on the other side of which it has been recorded as high as 1,600 m (Ridgely, 1976).

Although it lives chiefly in regions where the natural vegetation is rain forest, and Monroe (1968) found it common in Honduras within the dense forest itself, its presence there appears to be exceptional. In my experience, as in that of most of those who have written about the Blue Ground-Dove, it avoids the interior of heavy forest but frequents its borders, neighboring clearings and plantations, shady pastures, thickets, and light, open woods. It forages on the ground, often in company with other doves, but it frequently perches well up in trees. Although a number of Blue Ground-Doves may hunt together, they are not truly gregarious but fly singly or in twos and threes rather than in flocks.

Here in the Valley of El General, Blue Ground-Doves begin to repeat their soft *coo* or *coot* as the weather becomes drier in January, and they call much through the following three months. After rains become heavy in late April or May, they are less vocal; but I have occasionally heard their gentle notes until August. Although White-fronted Doves (*Leptotila verreauxi*) call amid foliage, Blue-Ground-Doves often choose high, exposed branches.

Early on 17 January 1965 a male perched for nearly three hours on dead branches about 23 m up, at the very top of a dying *Inga* shade tree in a small coffee plantation. Conspicuous against the sky, he continued through most of this long interval to call, but with decreasing frequency as the morning advanced. Soon after 7:00 on 20 January the dove alighted in the same dead treetop and called as persistently as on the previous morning. He seemed to be advertising his possession of territory and trying to attract a mate. Perhaps only the latter, for when another Blue Ground-Dove flew into an *Inga* tree about 18 m away and called for many minutes, the first dove appeared to ignore him instead of driving him away, as a bird defending territory would have done. When a Garden Thrush (*Turdus grayi*) alighted near the first dove, he moved to the dead top of a neighboring tree and remained there, calling, until I left half an hour later. No female of his kind appeared. In some years, although not in the year in which these observations were made, I found Blue Ground-Doves nesting in the coffee shrubs in this plantation. The failure of the calling male to drive away a potential rival was not unexpected, for I had occasionally seen two males in adult plumage flying together, apparently amicably, and even keeping closer company, as though they were a mated pair.

In March of a later year, a Blue Ground-Dove called persistently well within lofty rain forest. When finally I managed to glimpse him, he was perching conspicuously on a dead branch, about 36 m up at the very top of a leafless tree near the summit of a ridge. From this lofty perch, the dove was probably in view of neighboring clearings. For at least a quarter of an hour after I first heard him, he continued to call, then flew off over the treetops.

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When he attracts a female, the male may feed her by regurgitation, or at least go through the motions of doing so. One June I watched a male strut about on a horizontal branch at the edge of a thicket, turning rapidly to face now to one side, now to the opposite side. When a female alighted close beside him, he took her bill in his and appeared to feed her. Dropping her bill, he mounted her briefly, then stepped down to the branch on her other side and seemed to feed her again. Once more he stood on her back, after which he got down and took her bill in his from her left side, as at first. Then she flew away.

NEST AND EGGS

In El General, Blue Ground-Doves begin to nest in mid-February. The 30 nests that I have seen ranged in height from 115 cm to about 11 m, with 23 from 1.5 to 3.7 m up. Only three were below 1.5 m, and only four above 3.7 m. Most of these nests were placed in second-growth thickets and vine tangles. Eight were in coffee shrubs, three in orange trees, one in dooryard shrubbery, one in a clump of mistletoe, and one on the growing point of a tall tree fern.

On a nest just begun, with perhaps a half-dozen dry twiglets and flower stalks already laid upon the site, the blue and brown doves sat side by side for nearly a half-hour, each billing the feathers of the other's neck. At a later stage the female sits upon the growing nest, while her mate gathers straws, tendrils, and twiglets, usually from the ground, and brings them to her, mostly one at a time. Sometimes his slight burden is knocked from his bill as he passes through the maze of twigs and vines around the nest, but he does not retrieve it. When he reaches the growing structure, he usually stands upon the female's back, but sometimes beside her, while he lays his contribution in front of her or by her breast. Then he goes off to seek more material, while she arranges the pieces in the nest. At intervals she rotates to face in a different direction, while she continually bills the pieces in front of her to work them firmly into the structure. Spells of building sometimes last more than two hours. Although, as a rule, the male dove brings material and the female arranges it, sometimes he helps briefly with the latter; and at two nests I have seen a female bring pieces while her mate was incubating. She did not alight upon his back.

One nest was completed on the third day after it was begun, but by far the greater part of the work was done on the last two days. The completed nest is a slight, artless structure, even for a pigeon. Often it is hardly more than a narrow, concave platform made of fine twiglets, tendrils, rootlets, rachises of compound leaves, and the like, and so flimsy that the eggs are partly visible through the bottom. It measures about 10 cm in diameter.

I have records of 24 nests that contained two eggs or young. From one nest the first egg vanished on the day after it was laid. Two nests, both found in August, held each a single egg that may not have been the full set. In Trinidad, Belcher and Smooker (1936) found three sets of two eggs.

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At two nests the first egg was laid between 7:40 and 16:30. The second egg is laid two days after the first. At one nest it was laid between 7:30 and 9:15; at another between 7:00 and 10:00; at a third between 7:15 and 12:25; and at a fourth nest between 7:30 and 13:40.

The eggs are pure white. The measurements of eight eggs average 25.0 by 18.5 mm. Those showing the four extremes measured 26.2 by 19.1, 25.8 by 19.4, 22.0 by 17.8, and 26.2 by 17.5 mm.

In 30 nests in the Valley of El General eggs were present as follows: February, 5; March, 9; April, 10; July, 1; August, 3; September, 1; October, 1. The Blue Ground-Dove nests chiefly in the drier part of the year, from February to April. In May and June, when small birds of other kinds breed most freely, the dove suspends nesting, to resume it, on a reduced scale, in the rainy months from July to October. The same discontinuous pattern of breeding is exhibited by the White-fronted Dove and the Gray-chested Dove (*Leptotila cassinii*) in El General (Skutch, 1964).

INCUBATION

As in other pigeons, the first egg of the Blue Ground-Dove is covered much of the time, by one parent or the other, during the two days that elapse before the second egg is laid. In this interval I have found males on their nests at 7:30, earlier than they usually come after incubation is well established. Similarly, the female may return around midday, although she rarely comes to the nest so early after her set of eggs is complete. Apparently the doves cover the single egg without applying much heat to it, as the interval between the hatching of the first and second eggs may be as short as 2.5 hours, and I have not known it to exceed one day.

Incubation follows the pattern that is widespread, but not universal, in the pigeon family, with the male taking one long session each day, the female incubating all the rest of the time. As I have found at several nests, the male Blue Ground-Dove takes a smaller share of incubation than do males of the Band-tailed Pigeon (*Columba fasciata*), White-winged Dove (*Zenaida asiatica*), Ruddy Quail-Dove (*Geotrygon montana*), and Ruddy Ground-Dove (*Columbina talpacoti*), which incubate for from seven or eight to nine hours daily (Skutch, 1949, 1956, 1964), whereas he rarely does so for more than four to six hours. Usually the male Blue Ground-Dove comes to incubate between 8:30 and 9:30 and continues until the female returns between 13:30 and 14:30 (Skutch, 1959, Table 1, and later observations). Occasionally I have found him on the nest much later, once at 17:00 on a day when he arrived at 9:10. An exceptionally attentive male once came to incubate around 7:00, often around 8:00, and on three days he sat for more than seven hours. One day, when he was already covering the eggs at 7:50, his mate did not relieve him until 15:56 on the rainy afternoon, when he had been incubating for more than eight hours. After relieving the male in the afternoon the female remains in charge of the

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nest until he returns in the middle of the following morning.

Unless the nest is disturbed, interruptions to incubation are few and very brief. Especially toward the end of a long session, each partner may leave the nest for two or three minutes, rarely more than five. Since I noticed these breaks in nest attendance chiefly in hot, dry weather, I surmise that they are for the purpose of drinking—they are rarely long enough for foraging. Another possibility is that the dove flies off so briefly to avoid fouling the nest, although even before the eggs hatch the rim is often soiled with droppings.

Changeovers are effected without ceremony. The partner arriving to take its turn on the eggs usually alights on the supporting branch a short distance from the nest rather than close beside it. The sitting partner rises and walks out along a branch, on the opposite side, for 30 cm or more before taking wing. Then the new arrival, perhaps after preening a little, walks to the nest, slowly settles down, and adjusts the eggs beneath itself. The eggs are rarely left exposed for more than two or three minutes. By walking to and from the nest, rather than alighting on or taking flight from it, the doves avoid the risk of shaking the eggs from the frail, shallow receptacle. At one nest the male often cooed softly as he settled on the eggs and occasionally while he incubated. From his mate I rarely heard a note, except one morning when he came late to relieve her.

Efforts to learn exactly when the eggs hatch, as when they are laid, are attended by the risk of losing them, for the parent may cling to the nest until the observer comes very near, or until he shakes the supporting branch, then fly so abruptly that it knocks out an egg or two. My first successful attempt to learn the incubation period was nearly thwarted by this accident. On two of my visits the female left her low nest so suddenly that she threw out an egg, which fortunately fell upon dry leaves that prevented breakage, although the second time this happened it cracked slightly. Nevertheless, it hatched two days later, after an incubation period of approximately 14 days. At another nest the period was between 14 days 5 hours and 15 days. One egg was pipped more than 25 hours before it hatched, and another more than 32 hours. The parents promptly carry away and drop the empty shells.

NESTLINGS

The hatchlings' dark skins are liberally sprinkled over with the straw-colored, hairlike feathers typical of newly hatched pigeons. Their eyes are tightly closed. The bill is blackish, with the terminal two or three millimeters whitish. This light tip bears a well-developed egg tooth on the upper mandible and a minute but similar projection beneath the lower mandible, a short distance from the apex. The lower mandible projects slightly beyond the upper. When two or three days old nestlings can open their eyes widely. At seven days they bristle with long pinfeathers, and a day or two later their plumage has expanded, covering them fairly well.

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Unlike most birds who must go and find food after their first view of their nestlings, pigeons are prepared to feed them with secreted crop milk as soon as they hatch. At first the young pigeons are fed singly; but, after their eyes open, both nestlings rise up and place their bills inside the parent's mouth on opposite sides, and their heads bob up and down together as the adult regurgitates. The usual method of determining the rate of feeding by counting the number of times that parents bring food to the nest cannot be applied to pigeons and doves, especially when the nestlings are younger, for a parent may remain on the nest for many hours, regurgitating at intervals, when the young demand nourishment.

In 1948 I spent many hours at a conveniently situated nest watching the parents attend their young. During the nestlings' first four or five days each parent came to the nest once daily, at about the same hour that it was in the habit of arriving during incubation. On the day after these nestlings hatched a parent was constantly present, brooding them when not feeding them. The female regurgitated to them, always singly, about 14 times, for intervals ranging from about 40 seconds to 7 minutes and totaling 39 minutes. The male also fed them 14 times, for intervals ranging from 15 seconds to 3 minutes and totaling 16 minutes. Thus, the two nestlings received food in 28 installments, which together occupied 55 minutes. Two days later the female regurgitated to the three-day-old nestlings about 15 times, for intervals ranging from 20 seconds to 6 minutes and totaling 39 minutes. The male fed them 10 times, for intervals ranging from 1 to 9 minutes and totaling 42.5 minutes. Together the two parents fed about 25 times and were so engaged for 81.5 minutes. The young, whose eyes were opening, were sometimes fed simultaneously but mostly they received food singly.

When these two nestlings, six days old, had long pinfeathers and open eyes, they were not brooded except in the early morning, late afternoon, and night. Now, instead of coming to the nest only once a day, each parent came twice, the male twice in the morning, the female twice in the afternoon. The method of feeding the nestlings had changed greatly. The female delivered five meals that together occupied 12 minutes, and the male regurgitated only three times, for 11 minutes. The two parents together regurgitated eight times and were so engaged for a total of 23 minutes. Now the two nestlings were mostly fed simultaneously, but sometimes when one seemed to be satiated its sibling took nourishment alone.

A similar reduction in the number of acts of regurgitation and the total time devoted to this activity as the nestlings grow older has been observed in other pigeons, but the food now appears to be passed to the recipients more rapidly, and in larger quantities. The parent sooner exhausts the contents of its crop, and flies away if the nestlings do not require brooding. As the nestlings grow older they apparently receive less crop milk and more of the solid food that the parents have just gathered, as in the Wood-Pigeon (*Columba palumbus*) (Murton, 1965). During the nestling Blue Ground-Doves' first few days, their mother, after brooding them through the night, was able to feed them before she flew off to forage in the morning.

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By their sixth day she no longer fed them before her departure. The loss of these nestlings by predation prevented further observations.

Many years later, I watched parents attend a single week-old nestling throughout the day. It was hardly possible to determine the exact time devoted to feeding because on most bouts or spells of regurgitation the nestling's bill was not continuously in the parent's mouth but repeatedly in and out. Accordingly, the best I could do was to time the overall length of the bout. The male fed the nestling in 16 bouts, each lasting from about 10 seconds to five minutes, and totaling 19 minutes. The female fed only twice, each time for about two minutes. The 18 meals occupied 23 minutes. The female was with the nestling from daybreak until 6:22, when she did not feed, and from 14:50 until nightfall (excluding 23 minutes when alarm calls by neighboring birds caused her departure), when she fed twice. The male was on the nest from 6:25 until 7:46, when he fed seven times, and from 11:11 until 13:10, when he fed on nine occasions, most of them very brief. The nestling was alone from 7:46 to 11:11, and again from 13:10 to 14:50, during much of this interval in a hard rain.

While sitting with the nestlings each parent gently preened or billed their sprouting plumage. In contrast to White-fronted Doves and Ruddy Quail-Doves, Blue Ground-Doves do not clean the nest. Already soiled by the incubating parents, it becomes more heavily fouled while the nestlings are growing. These deposits may help to stabilize the flimsy structure, as has been observed in certain other birds careless of sanitation. Although distraction displays, often prolonged and vigorous, are widespread in the pigeon family, I have never seen a Blue Ground-Dove give one. Nevertheless, they take good care of their young. One female was found brooding, or at least sitting with her well-grown nestling in front of her, in the evening of its eleventh night, its last in the nest.

In my earlier paper on the Blue Ground-Dove (1959), I reported that two well-feathered young disappeared from their nest when only nine days old, and questioned whether they could have left alive. Although they had probably been disturbed, I believe it not impossible that they had flown or fluttered away. At a later nest one nestling died when a few days old and its corpse remained lying beneath its sibling. When the survivor was 11 or 12 days old I found it resting a few inches from its nest in a coffee bush. The next day it was on the nest's rim, and by the following day it had gone, aged 13 or 14 days. A nest built upon the growing point of a tree fern beside a road was pushed off by the growth of the young fronds and hung precariously. When I found it one nestling had vanished and the other, 11 days old, was perching nearby. When I returned later that day, one of the fledglings rose from the grassy roadway or low vegetation beside it. Although it flew weakly it easily kept ahead of me until it turned from the road into a thicket and vanished. At 11 days it seemed well able to escape all diurnal enemies except hawks. At a nest in an orange tree one nestling vanished and the other, when eight or nine days old and nearly feathered, was found on the ground where apparently it had passed

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the night. Replaced in its nest uninjured, it remained until it was 11 or 12 days old, when it left well clothed in plumage similar to the adult female's. It departed late on a rainy afternoon. Near this orange tree a few days later I noticed a young Blue Ground-Dove which flew well.

At a later nest, I watched events leading to a young dove's departure. Possibly it was somewhat precocious, as its sibling vanished a few days after hatching, and during its final days in the nest it received all the food that its parents brought. Dawn revealed the young dove sitting on the nest beside rather than beneath its attendant mother. When daylight grew stronger it preened. After a while it solicited food from its mother, who fed it intermittently for about four minutes. Then she preened it, after which it vigorously flapped its wings, then walked out on the supporting branch a few centimeters and returned to the nest. The mother sat with it until 7:15 but did not brood. When its father arrived at 8:20, it flew to a nearby branch. He called softly on the nest, then went to the fledgling about 60 cm away and fed it for four minutes. After this they continued for 20 minutes to rest side by side on the branch. The male parent flew away as the female alighted beside the young dove, but she did not stay. Soon the two parents sat close together higher in the tree, where the female preened her partner's head and neck for several minutes, until he departed. During the remainder of the morning the fledgling perched about 60 cm from the nest, panting with gular flutter when in sunshine. At noon it received another copious meal from its father, who remained close to it until the mother replaced him at 12:16. After a minute she left and the fledgling followed, flying strongly until beyond view. If, as was probable, this was the older of the two nestlings that hatched, its age was between 5 and 21 hours more than 11 days.

Young males resemble adult females. I have seen them molting into the blue adult plumage from early March to late June.

SUMMARY

In Costa Rica the Blue Ground-Dove lives chiefly in clearings and light, open woods in humid lowlands, where it hunts over the ground alone or with a few others.

In the dry season solitary males perch conspicuously in treetops, repeating a soft *coo* or *coot* for hours together, yet showing little territorial exclusiveness. Males alternately feed (actually or symbolically) and mount their mates.

In the Valley of El General these doves have two breeding seasons, the principal one in the drier weather from February to April, and a minor one in the wet months from July to October. Eggs have not been found in May and June, when the nesting season of most birds is at its peak.

The frail nest is built in trees, shrubs, or vine tangles from 115 cm to 11 m, but chiefly at heights of 1.5 to 3.7 m. Building follows the usual pattern of pigeons, the female sitting on the nest to receive and arrange pieces brought singly by her mate. Occasionally the male helps to shape

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the nest and, later, the female may bring material while he incubates. A nest was completed in three days.

Two pure white eggs are laid on alternate days. Two late nests held only a single egg.

The male incubates from four to six hours each day, rarely as much as eight hours, and the female all the rest of the time. The changeover is without ceremony. Unless disturbed, the doves walk to and from their nest, thereby avoiding the risk of knocking out the eggs as they take flight.

The incubation period is 14 to 15 days.

During the nestlings' first four or five days each parent came to the nest once daily, at about the same hour as it did during incubation. After this each parent came twice. At first the nestlings were fed singly, but after their eyes opened they inserted their bills into opposite sides of the parent's mouth and were fed simultaneously. As they grew older the number of acts of regurgitation and the total time devoted to feeding the young decreased, although the total amount of food delivered apparently increased.

Blue Ground-Doves neglect sanitation. Accumulated droppings may help to stabilize the flimsy nest. A distraction display was not observed.

Young sometimes fly spontaneously from the nest when 11 days and a few hours of age but may remain two or three days longer.

RUDDY QUAIL-DOVE

Geotrygon montana

A pigeon with a stout, quail-like body and short tail, the Ruddy Quail-Dove walks over deeply shaded ground with its slender bill inclined strongly downward. The male's upper plumage is rufous-chestnut, glossed with metallic reddish purple that glows richly in sunshine. His forehead is paler, and his pinkish cinnamon cheeks are bordered below by a broad brownish stripe. His throat and chest are vinaceous cinnamon, which fades to warm buff on the abdomen. The female's colors are more subdued, more brownish and olive, and her facial markings, in the pattern of the male's, are less distinct.

The Ruddy Quail-Dove inhabits humid forests from southeastern Mexico to Bolivia and Paraguay, and is one of the few small terrestrial birds that the Neotropical mainland shares with the West Indies, where it occurs only in the Greater Antilles. From the Central American lowlands it ranges upward in decreasing numbers to about 1,050 m, and has rarely been recorded as high as 1,400 m in Panama (Wetmore, 1968). In Venezuela it has been found up to 1,900 m in cloud forest (de Schauensee and Phelps, 1978). I usually meet it walking with bobbing head in front of me as I pass along a well-shaded woodland trail. When it becomes aware that it is being followed it steps off into dense undergrowth and vanishes; only when surprised at close range does it fly off through the underwood. Although often apparently

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reluctant to take wing, it flies strongly, sometimes passing swiftly across a clearing that separates patches of woodland.

When I first came to El General I seldom saw quail-doves outside heavy forest, but with the shrinkage of these woodlands it has taken increasingly to taller second-growth. Before sunrise, and on cloudy or rainy afternoons, I sometimes see one of these doves foraging over nearly bare ground in the shade of a grove of old orange trees beside our house, where it appears to find something edible in rotting fruits. Ruddy Quail-Doves appear to gather all their food from the ground, where they pick up fallen berries, seeds, and small invertebrates. Like most birds that rarely rise above the forest floor, they never flock but forage alone or in pairs.

In the Valley of El General the quail-dove utters its low, moaning *cooo* chiefly from March to June, when it nests. Although often the dove calls from the ground, it also does so from a perch. One day in early April I found a male resting about 8 m up (a height where it is rarely seen) in a small, vine-draped tree in tall second-growth woods. Here he repeated his sad note for many minutes, at the rate of 20 to 23 times per minute. This call is confusingly similar to that of the rufous-naped Gray-chested Dove (*Leptotila cassinii rufinucha*), which likewise frequents tall second-growth and older forests in El General, although it more often comes into the open and rarely penetrates as deeply into heavy forest as the quail-dove does. From the more resonant note of the White-fronted Dove (*Leptotila verreauxi*), the quail-dove's call is easily distinguished.

NEST

Although quail doves may begin to breed in early March, few pairs have nests before April. I have not watched the construction of nests, which, before they contain eggs, would be difficult to distinguish from random accumulations of fallen leaves and twigs caught up in the undergrowth. The 28 nests that I have seen were in old forest or tall second-growth, often amid dense undergrowth, at heights ranging from 45 cm to 2.7 m. Seventeen of these nests were 60 cm to 1.5 m above the ground; four were below 60 cm, and six above 1.5 m.

The sites were varied, as almost anything able to support such a loose construction may be chosen. A favorite site is the broad surface of a fallen palm frond that has lodged horizontally among bushes and vines of the undergrowth; six nests were so situated. A more secure foundation is provided by the broad, thick, clustered, living leaves of an epiphyte growing upon a trunk or, more rarely, a large rock. Three nests were on epiphytic aroids, two on the fern *Polypodium crassifolium* and one in a tank bromeliad. These six nests upon epiphytes included the three highest, at 2.5 and 2.7 m. Four nests rested upon the tops of low tree stumps. Seven nests were supported upon interlacing branches of low shrubs or tangles of vines. Careless of the stability of their nest's foundation, quail-doves often build upon dead branches precariously upheld by the undergrowth, upon an epiphyte attached

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to such a branch, or upon a bunch of big decaying leaves caught up on a low shrub. One nest was more securely situated in the center of a small tree fern's crown. One was in a privet hedge between a pasture and woods. Usually the nest is well screened by foliage and often it is close beside a tree trunk.

The nest is a slightly concave platform or mat of coarse dead twigs and petioles, covered with small leaves that may be either green or brown. The doves often bring green or fading leaves that wither in the nest. If supported on a stump or other firm base, the slight nest may consist of barely enough sticks and leaves to keep the eggs from touching wood or rolling off. It is often difficult to tell how much of the material was brought by the doves and how much fell upon the site from the trees above.

EGGS

Although I found no nest before it contained an egg, I discovered three with only the first egg of a set of two. In contrast to other pigeons, which cover their first white egg through much of the interval before the second is laid, quail-doves leave their less conspicuous, buffy egg exposed. On most of my visits to the three nests with a single newly laid egg, I found it unattended, cold, and wet. I do not know exactly when this first egg was laid. At three nests the second was laid more than 24 hours after I found the first. One of these second eggs was laid between 12:20 and 15:15; the other between 8:30 and 12:30. Apparently, second eggs are laid around midday.

Each of 27 nests contained two eggs or nestlings. One pair of doves, that had probably lost an egg before I found the nest, continued for nine days to incubate a single egg, which vanished before it hatched. The eggs are uniformly tinted with buff, which may be fairly deep, or rarely almost white. The measurements of 10 eggs averaged 27.6 by 20.2 mm. Those showing the four extremes were 29.4 by 19.4, 28.6 by 21.4, and 26.2 by 19.8 mm.

In the Valley of El General 29 sets of eggs were laid as follows: March, 2; April, 6; May, 9; June, 5; July, 5; August, 2. Elsewhere in northern tropical America the nesting season is much the same. In Trinidad six nests were recorded between February and July, three of them in May (French, 1973). In northern British Guiana (now Guyana) "the main nesting season was during the months of April and May, though it possibly commenced earlier (Beebe *et al.*, 1917). In Jamaica the quail-dove repeats its "sad moan" in March and April, an almost certain indication that it breeds then, although nestlings were found as late as June (Gosse, 1847). In El General the nesting season of the forest-dwelling quail-dove differs strikingly from that of its neighbors of clearings and thickets, the White-fronted Dove, the rufous-naped Gray-chested Dove, and the Blue Ground-Dove (*Claravis pretiosa*). The nesting of these three doves begins earlier in the year and is at its peak in March. In May and June, when nests

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of the Ruddy Quail-Dove are abundant, I have found none of the other three, which, however, resume nesting in July and continue on a reduced scale until September, rarely October.

INCUBATION

Ruddy Quail-Doves incubate in the pattern widespread in the pigeon family, with the female covering the nest from some time in the afternoon until she is relieved next morning by her mate, which then sits continuously, or at most with brief intermissions, until the female returns after midday. Thus, there are only two changeovers each day. On numerous visits to ten nests, the latest hour at which I have found the female on the nest in the morning was 8:40. Usually the male had replaced her before 8:00, and once before 6:35. At one nest he tended to come earliest at the beginning and end of the incubation period. Nearly always he continued to sit until after 15:00 and often until 16:00; one day he remained at his post until 16:57. At one nest I found that the female had already returned by 14:10, and at another by 14:40; but sometimes she remained absent until nearly 17:00. One evening I watched her replace her mate at 16:58. The male dove often continued on the eggs for eight to nine hours, which is much longer than some other male doves remain sitting. Male Blue Ground-Doves rarely incubate for more than four to six hours daily.

The incubating or brooding quail-dove was often surrounded by a swarm of mosquitoes that it tried to keep away by shaking its head and blinking its eyes. Each partner usually sat until it saw its mate walking over the ground toward the nest to relieve it. Then it would slowly rise from the eggs, step from the nest to the stump, leaf, or branch that supported it, and fly swiftly away low over the ground, in an almost horizontal course, until lost to view amid the undergrowth. The newcomer would continue to approach over the ground until two or three meters from the nest. Then, after a brief pause to look around, it would fly up to the nest and settle on the eggs. Usually the eggs were left exposed for only a minute or two at the changeover, but one morning the male did not take his place on the nest until eight minutes after his mate's departure.

Nearly always the dove coming to take its turn at incubation brought a contribution for the nest—often a green or dying leaf, more rarely a petiole or twiglet. On three of the four mornings when I watched a male arrive to begin his long spell, he brought something in his bill. Once, when I put him off the nest and then entered the blind, he picked up a leaf as he walked back and laid it on the nest. The female brought a leaf to the nest on each of the two afternoons when I watched her come to replace the male.

As I approach a nest the sitting dove of either sex compresses its feathers and leans forward, lowering its foreparts, elevating its hindparts, and raising its tail high above its back until, from a distance, it might be mistaken for another of the large dead leaves caught up in the surrounding tangle.

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In this cryptic posture, widespread among doves, the parent remains at its post until I come within a meter or so, often until I almost touch it. One male stuck to his nest and newly hatched nestlings while I shook the tree fern that supported them, but fled when my approaching hand was a few centimeters away. When finally the dove leaves it may fly or flutter more or less sharply down to the ground and walk away without displaying. Often, however, the dove of either sex limps slowly over the ground with raised wings beating loosely without coordination, or else fluttering wildly, in either case attracting attention and giving the impression that the actor is unable to fly. This distraction display may start near the nest or not until the retreating dove has alighted perhaps 15 m away, and it may continue for many meters until the performer has passed beyond view amid the undergrowth, sometimes as much as 30 m from the nest. These displays begin during incubation and are repeated while the nestlings are growing, but by no means consistently.

While watching from a blind I have seen the incubating or brooding dove assume the crouching posture when a squirrel passed close by the nest without appearing to notice it, and when domestic chickens scratched in the woodland about 15 m away. But when a party of Fiery-billed Araçaris (*Pteroglossus frantzii*) passed overhead, a brooding male took this attitude in the most extreme form, pressing his breast down against the nest and elevating his posterior parts until his tail pointed almost straight up. After the toucans drifted away the dove gradually resumed his usual sitting posture, with head bent slightly downward, body nearly horizontal, and tail inclined only slightly upward. The dove's crouching posture makes its light-colored forehead and breast less conspicuous, especially when viewed from above.

One egg was slightly pipped at least 18 hours before it hatched, and another was pipped more than 21 hours before the hatchling escaped. At a third nest I found the incubation period to be 10 or 11 days—the shortest that I had determined for any bird. At subsequent nests I have made two more accurate determinations. At one of these nests the interval between the laying of the last egg and hatching of the last nestling was between 11 days 2 hours and 11 days 18 hours, or 11 days 10 hours \pm 8 hours. At the other nest it was between 10 days 21 hours and 11 days 3.5 hours, or 11 days \pm 3 hours. As far as I know, no other dove has such a short incubation period.

NESTLINGS

Appearance.—Newly hatched quail-doves bear over much of their bodies rather long, straw-colored, hairlike down that fails to conceal their pink or flesh-colored skins. Their tightly closed eyes are blackish protuberances on the sides of their heads. The dusky bill becomes blacker toward the end, but the tip is whitish; and a hard, light-colored egg tooth covers the ends of both mandibles. The nestlings' legs and feet are flesh-colored.

Disposal of shells.—The empty shells soon vanish from the nest. I watched

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one male alternately break off and eat fragments of shell and feed his nestlings, which may thereby have ingested bits of it. On one occasion he held the shell in one side of his mouth while he regurgitated to a nestling on the other side. He took no less than three quarters of an hour to devour the large part of the shell, gulping down the last piece as though it hurt him.

Feeding.—Since in my earlier account of the Ruddy Quail-Dove (Skutch, 1949) I reported in detail studies of the care of nestlings from hatching until they left the nest, here I shall summarize my observations. Unlike most parent birds, the doves did not bring food to the nest each time they fed their offspring, but they continued to sit on the nest and at intervals regurgitated to them pigeon milk, probably mixed with other food, from the large supply that their crops appeared to hold, repeating this until the supply was exhausted. I counted as a separate feeding each time a parent took a nestling's bill into its mouth to regurgitate. Sightless day-old nestlings were mostly fed singly; but when two days old, with opening eyes, the two inserted their bills up to their eyes into opposite sides of the parent's mouth and were fed simultaneously. To end a feeding the parent shook the nestlings' bills out of its mouth.

As the nestlings grew older they were fed less frequently but seemed to receive more at each feeding. Day-old nestlings were fed 14 times by their father and eight times by their mother, making a total of 22 feedings in the course of a day. These feedings fell into three series, by the male between 8:03 and 10:26, by the female between 15:19 and 15:44, and again between 17:55 and 18:10 as the forest grew dark. Each feeding (while a bill remained continuously in a parent's mouth) lasted from a fraction of a minute to 3 or 4, rarely 5 or 6 minutes. The 14 feedings by the male lasted a total of about 21.5 minutes; the eight feedings by the female 23.5 minutes. Together the parents fed for 45 minutes.

When four days old the same two nestlings were fed three times by each parent, a total of six feedings. The male fed between 6:10 and 6:33; the female, between 13:46 and 14:22. The feedings by the male lasted 9, 4, and 2 minutes; those by the female, 15, 8, and 4 minutes. The nestlings' meals occupied a total of 42 minutes.

When seven days old these nestlings were fed once by their father and twice by their mother. The former fed from 7:49 to 7:59; the latter between 13:24 and 14:35. The male's single feeding lasted 10 minutes; those by the female six minutes each. The three feedings totaled 22 minutes.

If we assume that the two nestlings received equal attention from their parents, when one day old and nearly always fed singly, each was fed for about 22 minutes. When they were four days old and fed simultaneously, each received food for about 42 minutes, or nearly twice as long as when one day old. But when they were seven days old the time that each received food was about the same as when they were one day old.

At another nest the male held his two six-day-old nestlings' bills continuously in his mouth for 25 minutes, but in this long interval he regurgitated only

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intermittently, as was evident from the strong movements of his head and body, including alternate expansion and contraction of his chest. These efforts were separated by longer intervals of repose. Such intermittent regurgitation characterized most of the longer sessions of feeding.

At still another nest young almost ready to fly were in the course of a day fed once by their father, from 5:42 to 5:49, and twice by their mother, from 8:52 to 8:55 and from 17:31 to 17:34. The three feedings totaled only 13 minutes but appeared to be copious.

Brooding.—As the nestlings grew older the time they were brooded decreased rapidly. On the day after they hatched they were constantly attended. The male replaced the female at 5:45 and sat continuously until I suspended observations at 12:00. When I returned at 12:50 the female was on the nest, where she remained until nightfall.

When these nestlings were four days old the female left the nest at 6:03 and four minutes later the male flew up to it. He stayed until 10:48 when the female approached walking. Instead of promptly flying up to the nest, as on past mornings, she halted when about two meters away and stood in the same spot, immobile or at intervals preening, for nearly two and a half hours, then moved forward and delayed on the ground for another half hour. At 13:45 she finally went to the nest, where she sat through the wet afternoon until 16:57, when she left the nestlings exposed to hard rain. At 17:25 she returned in the rain and was still brooding when I stole away in the dark. Thus, four-day-old nestlings were unattended for a total of three and a half hours.

When the same nestlings were seven days old their mother, which in the past had waited on the nest until her mate came to relieve her in the early morning, left at 5:40, although he did not appear until 5:58. Instead of flying up to the nest, he walked past it and did not return for nearly two hours, while the nestlings remained alone. From 7:49 to 8:06 he accompanied and fed them. After his departure they were again alone until their mother joined them at 12:02. Then she sat through the rainy afternoon, with an absence from 16:50 to 17:19. The week-old nestlings were alone for six and a half hours, or slightly more than half the day. When rain did not fall they lay much of the time in front of, rather than beneath, the attendant parent, but often with their heads beneath the parent's breast, probably to shield them from the ravenous mosquitoes.

At a different nest young about nine days old were not brooded, although their mother sat facing them from 8:52 to 10:40 on a clear morning. Nevertheless, these nestlings were alone throughout the rainy afternoon until their mother arrived at nightfall. After feeding them she tried to brood, but found these nestlings too big to be covered comfortably. They stuck their heads beneath the ruffled feathers of her breast and remained so until I left them in the dusky forest, dripping with the continuing rain.

Sanitation.—In contrast to certain other pigeons, but like doves of the genus *Leptotila*, Ruddy Quail-Doves keep their nests scrupulously clean by eating all the droppings. Since they sometimes swallow them before feeding

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the nestlings, one wonders, as in the case of the shell that a parent ate, whether they avoid returning to the young doves some of their own wastes and, if so, how this is accomplished. The same question arises with certain other birds, such as the European Goldfinch (*Carduelis carduelis*) (Conder, 1948).

Development and behavior.—The nestling's development is amazingly rapid. When they are only two days old their eyes begin to open. By the following day their pinfeathers are sprouting, those of the remiges most conspicuously. By the seventh day after hatching the nestlings' plumage begins to break out of the horny sheaths. The expansion of the wing feathers, both remiges and coverts, is so rapid that by the following day the young are well covered as long as their wings are folded, but appear rather naked when the wings are raised. At eight days of age the nestlings' body feathers are only slightly expanded, while those of the head are tightly ensheathed. Two days later their bodies are well clothed but their heads are still nearly naked except for the bristly natal down and the sprouting pinfeathers. Their backs and wings are now deep olive-brown, variegated with deep buffy brown feather tips, that contrast sharply with the remainder of the feathers. Their eyes are dark brown and their queerly down-bent bills are blackish.

Nestlings only two days old hooked their bills over my fingers and tried to draw themselves up when they felt that they were slipping down. When hungry, tiny nestlings emerged from beneath the brooding parent and bobbed their heads around. Older nestlings rose up, peeping weakly, to run their bills over the parent's bill and face or to ruffle the feathers of its breast. However, unlike passerines, they did not gape for food the moment a parent arrived but, even after four hours without a meal, they might lie inertly in front of the newly arrived parent for many minutes until the adult was ready to regurgitate. Often they solicited without receiving anything, as the initiation of feeding appeared usually to be determined by the parent rather than by the young. After a meal older nestlings often flapped their wings vigorously or billed the feathers of the parent's breast while they peeped softly. The parents also billed the nestlings lying in front of them.

When a spot of sunshine, penetrating the high canopy of the forest, fell upon a nestling, it stretched up its head and panted violently while it moved restlessly over the nest, as though trying to escape the bright rays. When the first big drops of a hard shower struck feathered nestlings, they stood up and flapped their wings. This behavior was repeated when, after a rainless interval, the shower was renewed. One nestling walked out upon the long, spreading leaves of the aroid that supported the nest but soon rejoined its sibling. Then, as the downpour continued, both rested with their feathers puffed out and heads drawn in until their mother rejoined them in the twilight.

Departure.—Seven nestlings left four nests when 10 days old. Even when undisturbed none remained longer. As I approached one nest late in the morning an eight-day-old dove jumped to the ground. Caught and replaced it again dropped to the ground and started to walk steadily away. I overtook

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it and persuaded it to remain on its nest with its sibling, but in less than an hour it vanished. Its nest mate remained until 10 days old. At another nest the mother sat with two 10-day-old nestlings beside rather than beneath her until I came within about a meter. Then the three "exploded," each going in a different direction, and all flying so competently that they promptly vanished amid the underwood. No other bird that I have studied flew so well only 21 days after the egg from which it hatched was laid.

As I walked past a nest with two feathered nestlings a twig snapped sharply under foot, causing one of them to fly. The bird alighted on the ground a few meters away and did not move when I advanced to pick it up. As I replaced it in the nest the other hopped out and walked deliberately away until beyond view. The young dove that I had replaced in the nest promptly flew off again, but struck a twig and landed with its feet in the air. This time it stayed when replaced. One of these doves was a full 10 days old, the other about 9.5 days. At still another nest two young left, unwatched by me, between 8:00 and 9:30 of the tenth day after they hatched. Their nest was quite clean except for one last dropping and the ravelings of the feather sheaths, which small ants were carrying away.

On the day after its departure a young dove rose from near or on the ground as I passed by its empty nest. It flew low for about 9 m then walked rapidly away. When I followed it rose again, flew about 70 m, and vanished in the distance. At the age of only 11 days it seemed well able to escape most enemies except flying raptors.

NESTING SUCCESS

Ruddy Quail-Doves sometimes lay again after a successful nesting. A nest from which the last young departed on 17 June 1947 was covered with a few more leaves, some green and others brown, on which the first egg of a new set was laid on 19 July. The eggs in this nest hatched, but the nestlings survived no more than a day. Probably they were taken by the tayra (*Eira barbara*) or the opossum (*Didelphis marsupialis*) that I had seen near the nest on the day they hatched.

Of the seven species in the pigeon family at Los Cusingos, only the Ruddy Quail-Dove is truly at home in the depths of the rain forest. Among its adaptations for life in this habitat with many predators are the subdued colors of the adults; the slight, inconspicuous nest; the buffy eggs so rare in the pigeon family; the unusually short period of incubation; the cryptic comportment of incubating or brooding parents that do not move and thereby reveal their presence until a potential enemy has come very near; the cleanness of the nest; and the extraordinarily rapid development of the young which are feathered and can walk competently when only eight days old and fly well a day or two later. Nevertheless, only a minority of their nests are successful. In 17 nests, found at all stages, of which I know the outcome, at least 33 eggs were laid. Fourteen of these eggs hatched and 10 young survived to walk or fly away from five nests. Thus, only 29.4 per cent

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of the nests and 30.3 per cent of the eggs yielded fledglings.

Predators apparently destroyed most of the nests that failed. A number of feathers were scattered around the nest from which newly hatched nestlings vanished, but I detected no blood. Three nests with eggs were deserted, probably because a parent was lost or badly frightened. In two of these nests the abandoned eggs remained, fully exposed, for at least 10 or 11 days—an interval equal to the incubation period. While the cold, wet eggs lay neglected in one of these nests, the smaller, more cryptically colored eggs were taken from an attended nest of the Gray-headed Tanager (*Eucometis penicillata*) only two meters away. I have frequently been surprised by how long eggs remain in abandoned nests in woods or thickets, whereas many promptly disappear from well-attended nests. Apparently the activities or presence of the parent birds, or the warmth or scent of their eggs, give predators a clue that chilled and possibly also addled eggs do not provide.

SUMMARY

Alone or in pairs, never in flocks, Ruddy Quail-Doves walk over the ground in the deep shade of heavy rain forest or older second-growth. In dim light they may forage in more open situations, as beneath fruit trees in a quiet garden. Although reluctant to take wing unless closely pressed, they fly strongly. All their food appears to be gathered from the ground.

Their moaning *cooo* is often delivered from the ground, but occasionally from a perch as much as 8 m up. It is most often heard from March to June, and may be delivered for a long interval at the rate of about 20 times per minute.

In the Valley of El General eggs are laid from March to August, but chiefly from April to July. Two in number and buffy in color, they are deposited in slight nests built from 45 cm to 2.7 m up, but mostly from 60 cm to 1.5 m, on almost anything that will support them.

Each day the male incubates for one long session of eight or nine hours, and the female covers the eggs all the rest of the time. The incubation period of 11 days is extremely short for a pigeon.

While the nestlings are sightless, the parents regurgitate food to one at a time, but to both together after they can see to insert their bills into opposite sides of the feeder's mouth. The number of feedings and total time devoted to regurgitation decrease as the nestlings grow older.

Day-old nestlings were brooded continuously, and week-old nestlings for about half of the daytime. After this they were left exposed for long intervals, even while rain fell; but a parent attended them at night even after they were too big to be covered.

The parents keep the nest clean, swallowing the empty shells and all the nestlings' droppings. Often they do this shortly before they feed the nestlings and possibly return part of their wastes to them.

The nestling period is 10 days. At this age the young fly strongly, and

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appear well able to escape most enemies. If disturbed, eight-day-old young may jump from the nest and walk steadily away.

A month after their first brood flew a pair refurbished their nest and laid another set of eggs.

Five of 17 nests, or 29.4 per cent, each yielded two fledged young. Predation was the chief cause of loss.

Features rare in the pigeon family, such as the buffy eggs and extremely short incubation and nestling periods, adapt this widespread dove to survive in the lowest levels of tropical forest.



FIG. 2. Fork-tailed Woodnymph, *Thalurania furcata*.

Family TROCHILIDAE
RUFIOUS-TAILED HUMMINGBIRD

Amazilia tzacatl

Glittering green, with chestnut-brown tail and tail coverts, the Rufous-tailed Hummingbird is often the first member of its family to be noticed and identified by a bird watcher in the rainier parts of Mexico, Central America, or northwestern South America. It was the first bird whose nesting I studied, beginning in December 1928 in the Almirante Bay region on the Caribbean side of western Panama. My observations made here during the next six months, and continued the following year in the Lancetilla Valley, just inland from Tela on the Caribbean coast of Honduras, were published in my second ornithological paper under the bird's former name of Rieffer's Hummingbird (Skutch, 1931). A condensed version of this paper was included in Bent (1940). Through most of the last half century I have dwelt among these hummingbirds and recorded what, from time to time, I have learned about them. The present chapter is a synthesis of earlier and later observations on the habits of this highly successful species.

Ten centimeters or slightly less in length, *Amazilia tzacatl* is a hummingbird of medium size. Its rufous tail is tipped with bronze, and both the upper and under coverts are likewise rufous. The primaries and secondaries are black, slightly glossed with violet. Otherwise the bird is metallic green with the abdomen grayish. The female so closely resembles the male that the two are difficult to distinguish in the field, but the green of her throat and breast is paler because the feathers have whitish margins. In both sexes the upper mandible of the moderately long, slightly curved bill is largely black, becoming red at the base, while the basal half or more of the lower mandible is reddish, and the tip is blackish. Two males weighed 4.5 and 5.8 g, and three females 4.4, 4.6, and 4.7 g (Paynter, 1955). Weights given by other authors fall within these ranges, females being usually slightly lighter than males.

RANGE AND HABITAT

The species is found along the Caribbean side of Middle America from southern Tamaulipas, Mexico to Panama. In South America it occurs in the states of Zulia, Táchira, Mérida, Trujillo, and Lara in western Venezuela, in Colombia west of the eastern Andes, and in western Ecuador, where in 1940 I found it abundant as far south as Pasaje, El Oro. Beyond this its southward extension is stopped by the increasing aridity of the Pacific littoral. Altitudinally the Rufous-tailed Hummingbird ranges from the coast upward to 1,750 m in Oaxaca, Mexico (Friedmann *et al.*, 1950), 1,500 m in Guatemala (Land, 1970), 1,200 m in Honduras (Monroe, 1968), 1,825 m in Costa Rica (Carriker, 1910), 1,600 m in western Panama (Wetmore,

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1968), and at least 1,500 m in Venezuela, where I found it nesting in the Andes near Mérida.

In Central America this hummingbird is primarily an inhabitant of the wetter Caribbean side, while on the more arid Pacific side it is replaced by the related Cinnamon Hummingbird (*Amazilia rutila*). Nevertheless, wherever more humid conditions prevail on the Pacific slope the Rufous-tail establishes itself. In Costa Rica it is abundant in the rainy southern Pacific quadrant, until recently covered by heavy rain forest, where most of the observations here reported were made. It is not rare in the somewhat drier Central Tectonic Depression (more commonly but less correctly known as the Meseta Central or Central Valley). In the province of Guanacaste I found it abundant in November and December 1937, about Nicoya, where it mingled with the Cinnamon Hummingbird. Farther north in Guanacaste, where the low woods are largely leafless through a long, severe dry season, I and others have found Rufous-tails in spots of more luxuriant vegetation, as on land with a high water table. In the region of more abundant rainfall and heavier forest on the lower mountain slopes of northwestern Guatemala the species occurs sparingly in a small area, in the midst of the range of the Cinnamon Hummingbird (Land, 1970). In Panama the Rufous-tailed Hummingbird is widespread on the Pacific side, and extends to many of the offshore islands (Wetmore, 1968).

Wherever within this wide range showers are heavy and frequent enough to support verdure and flowering throughout the year, the Rufous-tail is a common resident in gardens, parks, plantations, shady pastures, open woodland, and along the forest's edge. Often it is the most abundant hummingbird. In regions of heavy rainfall and evergreen forests where the short dry season is in some years severe, it may become rare or absent at the height of the drought, when herbaceous and shrubby vegetation languishes and flowers are scarce. Although its true home is in the cleared lands, it may venture a hundred meters or more into fairly heavy rain forest to visit flowers in the more open spots, but I have never anywhere noticed it far within extensive tracts of forest, nor nesting in woodland.

FOOD AND DEFENSE OF FLOWERS

Like other hummingbirds the Rufous-tailed sips nectar from a great variety of flowers, of all colors from red to violet, and of all sizes from tiny florets to blossoms larger than itself. In dooryards and flower gardens it visits the big red flowers of hibiscus, the great, sky-blue, yellow-throated trumpets of *Thunbergia grandiflora*, and the small pink flowers of the coral vine (*Antigonon leptopus*). Through much of the rainy season, when the introduced flame-of-the-forest or African tulip tree (*Spathodea campanulata*) is ablaze with bloom, Rufous-tails gather to drink its nectar. When flowering orange trees fill the air with fragrance, these hummingbirds hover around them. In banana plantations they poise almost upright to thrust their bills upward into the long, slender, white flowers clustered beneath broad, thick, uplifted

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red bracts. When long hedges of *Stachytarpheta mutabilis*, a shrub of the verbena family, bloomed along three sides of our garden, Rufous-tailed and Violet-headed Hummingbirds (*Klais guimeti*) were the most abundant of the dozen members of the family that came to sip nectar from the little purple florets.

Among wild plants the narrow red floral tubes of *Hamelia patens*, a tall shrub of the madder or coffee family that is a troublesome weed in plantations and pastures, are at all seasons a dependable source of nectar. Another shrub of the same family, *Cephaelis elata*, draws these hummingbirds well into old forest to visit the small white florets clustered between two large red bracts. In August and September the acanthaceous shrub *Poikilacanthus macranthus*, more abundant in tall second-growth woodland on rich soil than in mature forest, attracts them with long, slender, lavender flowers. A large clump of these brittle shrubs was visited chiefly by Rufous-tailed Hummingbirds and Little Hermits (*Phaethornis longuemareus*). Although the latter consistently pierced the bases of the corollas, the Rufous-tail pushed its bill into the mouths of the flowers, the tubular part of which was nearly 4.5 cm long.

Other flowers are perforated by Rufous-tails. In the Cauca Valley of Colombia, Borrero (1972) watched them extracting nectar through holes in the bases of the golden trumpet flowers of the guayacán (*Tabebuia chrysantha*). He suggested that Rufous-tails, along with other hummingbirds and insects that stole nectar through perforations without transferring pollen, might benefit the guayacán trees by preventing the development of an excessive number of seed pods, which might snap off branches with their weight and drain food reserves. To reach the nectar of the large flowers of *Thunbergia grandiflora*, the Rufous-tail depends upon perforations made at the base of the tube by Bananaquits (*Coereba flaveola*). Although in the absence of these holes the nectar is unavailable to the hummingbirds, they try to chase the Bananaquits from the flowers. In the presence of *Amazilia* the honeycreeper seeks flowers in tangles of the vine which the hummingbird cannot easily reach (Borrero, 1965).

The extrafloral nectar cups of the epiphytic vine *Souroubea guianensis*, one at the base of each pale yellowish white flower of this member of the marcgravia family, provide much nectar for Rufous-tails and other hummingbirds. They extract the fluid without touching anthers or stigmas, while big bumblebees pollinate the flowers. The Rufous-tail that claims a cluster of these glossy-leaved vines tries to drive other visitors away.

The most vigorously and consistently defended flowering plants that I have noticed were six tall shrubs of the rubiaceous *Palicourea guianensis* growing in front of my study window, all in a radius of about 6 m. In May, when these shrubs were profusely adorned with erect panicles of small, bright yellow, tubular flowers on orange stalks—a lovely display against the large, prominently veined leaves—two Rufous-tailed Hummingbirds claimed them. One took possession of the three nearest the window while the other defended the farther three, beside a clump of tall timber bamboos.

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The branches of the second trio that came closest to the nearer trio were a neutral zone, where either hummingbird might visit the flowers without being disturbed by the other. Neither protested when it saw the other probing his neighbor's own flowers. Any other hummingbird that intruded among these shrubs was chased away, usually by the one whose area it had invaded, but sometimes, especially if it entered the neutral zone, by both Rufous-tails together. Trespassers that were chased included a Violet-headed Hummingbird, a Snowy-breasted (*Amazilia edward*), and a wandering Rufous-tail. With the exception of nectar-sipping Bananaquits, birds other than hummingbirds were not molested.

The larger nectar-drinking insects were not tolerated by the Rufous-tails. Repeatedly I saw them drive away big bees and middle-sized butterflies. One morning the excited notes of the Rufous-tail nearest my window caused me to look out in time to see it darting at a black bumblebee that was visiting its flowers. Since the insect did not promptly flee, the hummingbird dashed at it again and again, sometimes almost touching it, until the black intruder retreated. When an invader resisted immediate eviction the hummingbird twittered excitedly, with notes hardly distinguishable from those that a female utters when her nest or young appear to be in peril. Sometimes the hummingbird complained in this manner when I walked among the *Palicourea* shrubs. Smaller insects, about the size of stingless meliponine bees or houseflies, were ignored by the hummingbirds even when they visited the flowers, but midge-sized insects were caught on the wing and eaten.

In Colombia, Borrero (1972) watched Rufous-tails behave aggressively toward bees and butterflies that visited defended flowers. In the Caribbean lowlands of Costa Rica a Rufous-tail chased skipper butterflies (Hesperiidae) from the middle and upper parts of a flowering *Stachytarpheta* hedge (Primack and Howe, 1975). Boyden (1978) counted the number of times a Rufous-tailed Hummingbird chased other hummingbirds and large bees from defended pagoda plants (*Isertia haenkaeana*) in Panama, and considered the bird's energy balance.

The Rufous-tail nearest my window surveyed its flowers from a dead twig near the top of its tallest shrub. Every few minutes it took wing to visit the yellow flowers, devoting only a second or two to each and probing a number on a single round. When it returned to perch its dark bill was liberally dusted with pale pollen. If it had not so often wiped its bill against a twig to remove some of this encumbrance, it would have been a more effective pollinator. Nevertheless, enough grains remained to fertilize the next flower it visited. Occasionally the Rufous-tail chirped weakly or sang in an undertone, as I surmised from the way its throat swelled out, although I could hear nothing at such times. At intervals it rose into the air to dart back and forth in short flights with frequent reversals, catching minute insects. Returning to its watch-post it might preen or scratch its head with a foot raised above a relaxed wing, in the manner of passerine birds. It was seldom still for two consecutive minutes.

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By the second week of June, when the *Palicourea* shrubs were passing from bloom, a single Rufous-tail defended all six of them, having evidently displaced its neighbor in a contest that involved much excited twittering. By late June, when few flowers remained, the hummingbird spent little time among the shrubs.

When my *Stachytarpheta* hedge was blooming profusely and visited by many kinds of hummingbirds, I saw frequent chases, both intra- and interspecific, which rarely resulted in contact, but I noticed no consistent defense. The abundance of flowers, coupled with the multitude of visitors, evidently made such defense unnecessary or futile. In my experience, Rufous-tails only exceptionally find sources of nectar sufficiently rich and compact to be defended. Much of their nectar gleaned is from flowers too widely dispersed to be guarded, as is true when they visit shrubs of *Cephaelis* scattered through woodland, each with relatively few open blossoms.

Although the hummingbirds' defense of flowering plants is commonly included in the broad category of "territoriality," it differs greatly from other manifestations of this behavior, even from the defense of feeding territories. A feeding territory, properly so-called, is an area which a bird defends over an extended period for whatever food it will yield for its holder, perhaps a succession of flowers or fruits of different species, or a changing variety of insects. Examples of such territories are the winter territories of Common Mockingbirds (*Mimus polyglottos*), Summer Tanagers (*Piranga rubra*) wintering in tropical America, and many others. Like a number of other hummingbirds, the Rufous-tail does not try to defend a plot of ground over an extended period, but only flowers presently yielding nectar. As soon as these become scarce it moves to other sources of nectar, which it may be forced to share with other hummingbirds. Moreover, it tries to evict a wider range of animals than does any truly territorial bird of which I have knowledge, including all that take nectar, except the smaller meliponine bees that it probably does not regard as important competitors. The hummingbird is more like a man who prevents other people, dogs, crows, and the like from stealing his dinner than the owner of a landed estate trying to keep out trespassers. Stiles (1973) pointed out the very different behavior of Anna's Hummingbirds (*Colypte anna*) when they defend breeding territories, which are true territories, and when they defend flowers. Like many other tropical American hummingbirds, the male Rufous-tail does not defend a breeding territory, but only his singing post in an assembly.

In addition to nectar from the most diverse flowers and insects caught in the air, Rufous-tails glean minute creatures from bark and leaves.

BATHING

Rufous-tailed Hummingbirds bathe by sliding with beating wings over the broad, flat, horizontal surface of a leaf, such as that of the banana plant, which is wet with rain or dew. Or else they cling to a wet cushion of green moss growing on a trunk, push their breasts and rub their faces against

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it, until their plumage is well soaked. After its bath the bird perches nearby and vigorously shakes its relaxed plumage. I cannot recall having seen this species bathe by dipping momentarily into brooks or pools, a method preferred by woodland hummingbirds, but I watched one bathe in the water that had collected in a tank bromeliad on a tree.

VOICE AND COURTSHIP

The most frequently heard utterance of the Rufous-tailed Hummingbird is a rapid sequence of slight, sharp notes that might be described as a twitter. It is continued for minutes with hardly a pause when the bird is disturbed or alarmed, as when a competitor visits its defended flowers or, even more, by the approach of a potential enemy to its nest or fledged young. Very different is a series of high, plaintive notes ascending in pitch and too rapid to be counted accurately. Sometimes I seem to detect seven or eight notes in the sequence, but often it is shorter. The first two or three notes, lower and more prolonged than the others, are sometimes voiced alone. This distinctive utterance is sometimes given by a perching Rufous-tail but is more often delivered in flight, especially while a number of individuals hover around profusely flowering trees or shrubs, or while one chases another. Although heard in all months, here in El General it is most frequent from August to October, as the principal breeding season approaches.

Different again is the slight song that is delivered almost exclusively in the courtship assemblies, a quaint, subdued utterance that lacks the variety and animation of the courtship songs of certain other hummingbirds. It sounds something like *tse we ts' we*, and a longer version might be written *tse we ts' we tse we*. Or, if one prefers words, *right up that tree* rapidly uttered, at least suggests its cadence. Like the dawn songs of flycatchers, these notes are heard chiefly from dawn until around sunrise, rarely later in the day.

I have found three singing assemblies or leks of the Rufous-tailed Hummingbird. The first, discovered in December 1935, was situated at the forest's edge beside a bushy neglected clearing on a steep slope above the Río Buena Vista, at about 900 m on the Pacific side of southern Costa Rica. The gathering consisted of at least three birds, one of which perched on a twig in a fallen treetop, 2 m above the ground. After falling silent during the driest months, these hummingbirds resumed singing after the return of the rains. In October one of them was performing in almost the same place where I had found him singing in the preceding December. My notes on this assembly are scanty.

The second assembly was in the dooryard of a farmhouse in the Pejivalle Valley in the Caribbean drainage of Costa Rica, at about 600 m. It was situated near the flowering *Stachytarpheta* hedge that bordered the enclosure. Early on cool April mornings several males perched conspicuously on slender dead twigs at no great height, repeating over and over dry little songs slightly different from those that I had heard on the opposite side of the

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Cordillera de Talamanca. In other species of hummingbirds, even in the same locality, different assemblies may have surprisingly different songs (e.g., Skutch, *in* Bent, 1940).

From 1942 until 1963 I kept notes on a singing assembly close by our house. Year after year, from two to four Rufous-tails proclaimed their presence on nearly the same stations, close by the hedge along the western side of the garden. Perching conspicuously on slender dead twigs of guava (*Psidium Guajava*) or burío (*Heliocarpus* sp.) trees, from about 3 to 6 m up, each tirelessly sang *tse-we ts'-we* in a slight, sharp voice, from the dim early dawn until a little before or shortly after sunrise, according to the season. Only at this time was their singing sustained; later in the day I heard at most brief snatches or isolated phrases. In 1943, when I made a plan of the hummingbirds' stations, those of the three persistent performers were from 15 to 22 m apart, while a fourth, which sang less constantly and ceased earlier in the year, was nearer one of the others.

When I first became aware of this assembly, and for the next few years, it was close beside a flowering *Stachytarpheta* hedge. The hummingbirds interrupted their singing to visit the flowers, rarely for more than five or six seconds at a time. The moment one had sipped nectar from the last purple floret he returned to his perch to resume his song. Intervals of foraging were much shorter than those of sustained singing. These Rufous-tails seemed to interrupt their declamations just long enough to moisten their throats. After sunrise, when their songs became more widely spaced and soon ceased altogether, they made longer visits to the flowers. On their display perches these hummingbirds were shier and more difficult to watch than when they gathered nectar.

Often a Rufous-tail stopped singing long enough to rise into a clear space near his guava tree and hover for a few seconds from 6 to 10 m above the ground, then quickly return to one of his perches. This appeared to be a display, for the bird did not dart around catching volitant insects; but it was far less spectacular than the flight displays of several species of northern hummingbirds. As at the assemblies of other kinds of hummingbirds that I have watched, I failed to witness mating. Frequently a second Rufous-tail, of undetermined sex, suddenly alighted near one of the performers, giving rise to a dashing aerial pursuit, in which a third individual often joined. The flying birds promptly vanished amid the foliage.

Although the songfulness of these hummingbirds might diminish in very wet weather, it rarely ceased completely during the rainy season. They continued to perform every morning through the flowery months of December and January, when vegetation flourished despite diminished rainfall, and into the increasing drought of February. Rarely, as in 1952, they stopped singing in the first week of February, but more often they continued into the second half of the month and sometimes, as in 1947 and 1950, into the first week of March.

Usually singing was resumed in April after the first showers that broke the drought, but sometimes not until early in rainy May. The shortest interval

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of silence that I recorded was from 2 March to 7 April in 1947, a year when several generous showers fell in March; the longest, from 15 February to 8 May in 1949, when March was drier. Accordingly, this assembly was active throughout the year except for an interval of from little over one month to nearly three months, at the height of the dry season and while vegetation was recovering from its effects. In El General, I have found nests in which eggs were laid in every month except February, March, April, and September.

Since in temperate North America the defense of flowers by hummingbirds is much better known than singing assemblies, certain ornithologists have suggested that these Rufous-tails were performing to proclaim "feeding territories" rather than to attract mates. The fact that two of the three assemblies that I have found were beside *Stachytarpheta* hedges whose flowers supplied much nectar lends some weight to the former interpretation. However, many facts tell against it. The behavior of these hummingbirds was very different from that of those defending the *Palicourea* shrubs, as earlier described. The Rufous-tails in the assembly were at their stations only until sunrise, or a little later; those at the *Palicourea* through much of the day. The latter did not sing *tse-we ts'-we*, as the former persistently did. One of the birds in the assembly was stationed 15 m from the *Stachytarpheta*, with another directly between him and the hedge, his nearest source of nectar—an arrangement that was stable. In the early morning, when the hummingbirds sang, their visits to the flowers were very brief; later, after song ceased, they devoted much more time to the *Stachytarpheta* blossoms.

In late February, March, and April when these birds no longer occupied their singing posts, the *Stachytarpheta* hedge, although blooming less profusely than at other seasons, was one of the best sources of nectar, for the flowering of native shrubs and herbs was then at lowest ebb. Thus, just at the time when, according to the "feeding-territory" hypothesis, it was most urgent for the Rufous-tails to defend their resources, they neglected to do so. Moreover, this assembly was maintained in the same spot for 15 years after the *Stachytarpheta* was replaced by a privet hedge that never flowered because it was kept pruned. To continue in a spot that must have been well known to all the female Rufous-tails in the vicinity was more important to these males than to be close to a source of nectar.

Finally, the birds in the assembly and those at the *Palicourea* treated other species very differently. The latter would not tolerate any nectar-drinking bird or large insect near their flowers. Those in the assembly usually sang in apparent indifference while hummingbirds of other kinds visited the flowers nearest their stations; chases were rare. One Rufous-tail continued calmly to sing while a White-necked Jacobin (*Florisuga mellivora*) rested for about one minute in his guava tree. Many other kinds of tropical hummingbirds sing, often all day long, in assemblies which are by no means always situated near rich sources of nectar. It is now generally recognized that

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these gatherings, like other leks, serve to attract females that come to have their eggs fertilized (Skutch, 1973).

NESTS

The 63 nests of which I have records, from localities ranging from northern Guatemala to western Venezuela but chiefly in the Valley of El General in Costa Rica, were all in fairly open situations, including ornamental plantings around homes and public buildings, orchards, coffee plantations, bushy pastures, scattered trees in clearings, hedgerows, and roadside trees or shrubs; none was in woodland. Trees that supported nests included orange and other citrus, rose apple (*Eugenia Jambos*), cashew (*Anacardium occidentale*), guava, mango (*Mangifera indica*), and cypress (*Cupressus lusitanica*); among shrubs were coffee, hibiscus, bougainvillea, and the weedy tuete (*Vernonia patens*). Rarely a tall herb, such as ramie (*Boehmeria nivea*) or the weedy mint *Hyptis capitata*, was chosen as the nest site. Several nests were in bamboos. One nest was at the tip of a drooping slender vine, supported by an ascending branchlet, and several were on thin hanging branches of trees or shrubs. A most exceptional nest was in the broad, cuplike axil of a leaf of maize, just below the tassel, of a plant standing well within the cornfield. Although usually the nest was on a slender twig, sometimes it was attached to the petiole of a simple leaf or to a compound leaf, as of a palm, tree fern, Brazilian rubber tree (*Hevea brasiliensis*), or akee tree (*Blighia sapida*). This list, which might be greatly extended, is sufficient to indicate the wide variety of sites that *Amazilia* chooses, and the frequent choice of cultivated plants.

An adequate nest site consists of a nearly horizontal perch, slender enough to be grasped by the hummingbird's tiny feet, beside or in the midst of twigs, petioles, or other leaf parts that give lateral support. Sometimes a long thorn of a citrus tree provides the perch, while the stem from which the thorn grows serves for lateral attachment. The nest is usually in a more or less exposed situation that the hummingbird can reach in flight rather than amid dense foliage, and is inconspicuous chiefly because of its small size and its color that matches the surroundings. None that I have seen was saddled on a thick branch, like the nests of certain other hummingbirds.

The 45 nests of which I recorded the heights ranged from 1 to 6 m above the ground. Twenty-two of these nests were from 1.5 to 2.5 m, eleven from 2.8 to 4.5 m, and five from 5 to 6 m. Only seven were below 1.5 m. A nest started barely 60 cm up in a small citrus tree vanished before completion.

As in all species of hummingbirds that have been adequately studied, the female builds her nest with no help from a mate. The first step in construction is the attachment of a bit of material in the chosen site. This may be a tuft of seed down, strips of thin papery epidermis from a banana plant, dry fragments of grass, or anything small, soft, and pliable. It is fastened to the support by cobweb, which may be collected from walls of

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houses as well as from vegetation, and sometimes also by pieces of thread, hairs from horses or cattle, or vegetable fibers. Some builders pulled strands of hemp from a decaying cord. From the beginning the Rufous-tails that I watched alighted on the nest to add another contribution, instead of hovering on wing in the manner of hermit hummingbirds which attach their nests to slippery tips of palm fronds or strips of banana leaf that provide no perch.

After pushing in a new bit of material the builder usually proceeds to shape her structure, bending down her head to press the underside of her bill against the outside, often revolving to draw the yielding stuff inward against her breast from all sides. While so engaged she may erect the bronzy green feathers of her crown and vibrate her wings. Then she may sit facing in one direction while her body bounces up and down in a way that suggests that she is kneading the materials with her feet. She may hover beside the nest to remove a loose bit of material from the outside, then take it into the cup. Sometimes she flies off, only to return promptly with empty bill to sit on her nest and resume the operation of shaping it; she may do this repeatedly. By these movements the nest cup is molded closely to her lower breast and abdomen, leaving the upper part of her body, head, neck, wings, and tail outside—a situation that will have interesting consequences as her nestlings grow.

The building hummingbird brings the various constituents of her nest in no fixed order. Soft down, which is used chiefly for lining, may be added at an early stage, or even start off the nest. Lichens, which appear to be the finishing touch, are often attached to the outside before the completion of the walls that they adorn.

It is difficult to tell when a hummingbird's nest is finished, for she continues to add to it during the incubation period, especially in the morning after the sun warms the air, when sessions on the eggs tend to be short and absences to forage or gather material frequent. At one nest seven days elapsed from the start of building to the laying of the first egg; at another nest at least seven days; while at two nests the interval was 12 days. During four days of one of these 12-day intervals, little work was done because almost continuous hard rain kept the nest soaked and discouraged building.

Some nests are not completed because the builder, apparently an inexperienced young bird, chooses an inadequate site. One Rufous-tail attached her nest to a slender, branchless, horizontal twig of a riverwood tree (*Pithecolobium longifolium*). Lacking a lateral support, the structure pivoted sideways, grew lopsided, and was abandoned as useless. Another Rufous-tail tried to build in the angle formed where the tip of a leaf happened to touch a neighboring branch. The unattached leaf apex slipped down and frustrated her efforts. Although I have seen nests built successfully in the axil of a leaf, resting on the petiole, the opposite end of a leaf is obviously an inadequate foundation for any bird that cannot fasten her structure beneath it, as hermit hummingbirds do. Rarely a nest is built atop an older nest.

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The completed nest is a tiny open cup with soft, thick walls incurved at the top, making it difficult for the eggs to roll out. It is composed of shredded plant fibers, weathered strips of grass, fragments of decaying leaves, and much soft, downy material, usually from seed plumes, which, thickly felted, forms the lining. The down may be whitish, buffy, or tawny. Rarely large, brownish scales (ramenta) from the fronds of tree ferns are a major ingredient. Exceptional nests contain a few small, downy feathers. The outside is usually adorned with many small, grayish green foliaceous lichens, along with more or less green moss, which may dangle below it in waving festoons. Occasionally liverworts are attached instead of moss. Rarely lichens and moss are so sparingly applied that the prevailing color of the exterior is grayish or tawny from the fibers and down in the walls. Sometimes the beauty of an otherwise well-built nest is marred by a long, withered grass blade used in the foundation and carelessly permitted to hang beneath it. Liberal amounts of cobweb bind all these materials together. Nests vary from 3 to 5 cm in height; 45 to 49 mm in external diameter. The internal measurements are: depth 19 to 25 mm; diameter 29 to 32 mm.

EGGS

I have never seen more than two eggs in a Rufous-tail's nest. A few with one egg had probably lost another. An interval of approximately two days separates the laying of the first and second eggs, as in other hummingbirds. I have not accurately timed the laying of first eggs. In six nests the second egg was laid before 7:15. Of these one was laid before 5:40; one between 5:25 and 6:00; one between 5:45 and 6:35; and another before 6:35.

The tiny white eggs are the long, narrow ellipsoids typical of hummingbirds. Eight eggs averaged 14.0 by 8.8 mm. Those showing the four extremes measured 14.3 by 8.7, 13.9 by 9.1, and 13.5 by 8.7 mm. Despite the small volume and consequently relatively great surface of hummingbirds' eggs, their paper-thin shells are relatively the lightest found among birds. Their weight is only 4.2 per cent of the eggs, whereas the average for birds as a whole is 8 per cent (Meise, 1956).

In the Valley of El General 33 sets of eggs were laid as follows: January, 3; May, 3; June, 3; July, 5; August, 2; October, 3; November, 3; December, 11. Thus, the Rufous-tail lays throughout the year except at the height of the dry season in February and March, and while vegetation is recovering from its effects in April. In December and January, when Rufous-tails' nests with eggs or young are found in greatest numbers, bright sunshine and soil that still retains much moisture unite to produce the year's greatest profusion of flowering herbs and shrubs, which yield abundant nectar for the nestlings. Nevertheless, the bird can reproduce successfully beneath the cloudy skies and long-continued deluges of October and November, although at this time nestlings develop more slowly.

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On the Caribbean side of Central America, where the dry season is less pronounced, Rufous-tails appear to breed most freely in the very months when they do not nest on the Pacific slope. Near sea level in the Almirante Bay region of western Panama, where I resided from late November 1928 until early in the following June, I found 13 nests in which eggs were laid as follows: January, 2; February, 7; March, 2; April, 2 (Skutch, 1931). Farther north, in Caribbean Honduras and Guatemala, I have found nests with eggs in February, May, June, August, September, and December. For British Honduras (now Belize) Russell (1964) reported occupied nests in January, February, May, August, and September. A nest that I found near Cartago, Costa Rica, at about 1,400 m, held, on 3 November 1935, two well-feathered nestlings that evidently hatched from eggs laid in late September. Although the Caribbean population, as a whole, nests throughout the year, I do not know how long any individual female continues to reproduce.

On 11 March 1974 a Rufous-tail was incubating in a nest that I found 6 m up in an introduced cypress tree near Mérida, Venezuela at about 1,500 m.

INCUBATION

Of all the nests of *Amazilia tzacatl* that I have seen, the most favorable for observation was the first, built on the petiole of a low ramie plant just in front of the screened window at which I sat poring over microscopic preparations of the banana plant, near Almirante in 1928 and 1929. At this nest, in which two sets of eggs were hatched and one brood fledged, I never saw two individuals in attendance, from which I concluded that only the female incubates, broods, and feeds the young—a conclusion that in later years I have found no reason to doubt.

On 12 December 1979, Marie Cole alternated with me in an all-day watch at a nest with two eggs five days from hatching. The hummingbird started the day by leaving the nest when the light was too dim to see her go. She returned for the night at 17:14, 20 minutes before dark. In a day of little less than 12 hours, we timed 14 sessions, ranging from 4 to 162 minutes and averaging 38.6 minutes. An equal number of recesses varied from 6 to 25 minutes and averaged 11.4 minutes. Her session of nearly three hours spanned the middle of the day. After an outing of only seven minutes, this was followed by a session of 91 minutes in early afternoon, then by one of 45 minutes in mid-afternoon. Her next longest interval on the nest was only 39 minutes, before the middle of the morning. She covered her eggs for 77 per cent of the day.

In the forenoon this female added material to her nest on five of her returns to resume incubation. When bright sunshine fell upon her, she panted with open mouth. When Cinnamon-bellied Squirrels (*Sciurus grana-tensis*) passed within 6 or 9 m of the nest, she repeatedly darted at them, almost touching them, until they retreated into a neighboring thicket. She

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also darted toward and around a large lizard at the same distance from the nest. Another female tried vainly to drive away a big lizard that had climbed almost to her nest; even when she appeared to strike it with her bill, it refused to budge. More successful with a Groove-billed Ani (*Crotophaga sulcirostris*), she chased it for 15 m.

Before laying her second egg the female sits on her first egg sporadically by day, and at least at one nest she slept upon it during the two nights that passed before the set was complete. The early start of at least partial incubation results in asynchronous hatching, the first egg often hatching in the afternoon, the second during the following night or early next morning. At seven nests the incubation period, counting from the laying of the second egg to the hatching of the second nestling, was not less than 15.5 days nor more than 16 days plus a few hours. Assuming that the second egg hatched early in the morning, when at several nests the second nestling was first seen, rather than during the preceding night, the incubation period was very nearly 16 full days.

The empty shells are not promptly removed and often some or all of them remain crushed against the bottom of the nest.

NESTLINGS

Appearance and behavior.—Despite an incubation period long for so small a bird, the nestlings hatch in a very underdeveloped state. The grublike creature is blackish above, pink below, with the tarsi, toes, and short stubs of wings pale gray. The dark skin of the back, hindneck, and top of the head is wrinkled. It is naked except for a row of eight tufts of tawny down along each side of the mid-dorsal line. The rudimentary bill, a short protuberance at the front of the head, bears near the tip of the upper mandible a minute whitish egg tooth, hardly visible without magnification. The eyes are tightly closed. Soon after hatching the nestlings gape like passerine nestlings, at intervals lifting their heads straight up and revealing yellow or orange-yellow inside the mouth. Sometimes they stretch up so vigorously that they tumble over on their backs, whereupon many of their internal organs, including the remnant of the yolk sac, are visible through the transparent skin. Unlike many passerine nestlings, those that I tested did not gape when I gently shook their nest. Only by lightly prodding their chins with a very fine twig could I elicit gaping during their first few days. At most they responded slowly, and sometimes not at all.

When the nestlings are six to eight days old their beady eyes open, and on the head and back the tawny tips of feathers begin to protrude from the ends of their short sheaths. At the age of two weeks the nestlings are fairly well clothed with feathers which, if disturbed, they erect until they bristle. With bills that have become much longer they may try to bite the finger that touches them. Their tails are still rudimentary. They will remain in the nest a week or ten days longer.

Feeding.—The female hummingbird begins to feed her nestlings very soon

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after they hatch. Arriving without visible food, she perches on the nest's rim, thrusts her long bill well down into a nestling's throat, and with convulsive movements regurgitates part of the contents of her crop. Usually she gives to both nestlings each time she returns to feed, and often she regurgitates to each twice, alternately. After the nestlings are older each may receive food four times on a single visit. At the conclusion of a meal the mother often thrusts out her long, white tongue several times while she sits brooding.

In July 1976 I recorded the rate of feeding at a nest with two young. When they were, respectively, three and four days old, their mother brought food to them nine times during the first six hours of the day, 5:07 to 11:07. This was much less than the number of times that she came to the nest to brood. When these two nestlings were nine and 10 days old, she brought them food 13 times during the same hours of the day. The intervals between meals ranged from 15 to 56 minutes. Each feeding visit lasted from about 30 to 40 seconds, but the delivery of food to the two nestlings was not continuous throughout this interval, as the parent removed her bill briefly from their mouths between acts of regurgitation. On this day she came to the nest only to feed. When the nestlings were 15 and 16 days old, they received 14 meals in the first six hours of the day. The intervals between meals now ranged from 10 to 52 minutes. Feedings lasted from 17 to 31 seconds and were not continuous. A single act of regurgitation tended to take longer than it did six days earlier. Again, the parent was at the nest only long enough to deliver the meal. On this morning she first came with food at 5:16, when the light was still so dim that she was barely visible through 8 × 40 binoculars.

Although the hourly rates of feeding on these three days were only 0.75, 1.1, and 1.2 times per nestling, similarly low rates are usual among hummingbirds (Skutch, 1973). Indeed, all birds that feed by regurgitation tend to do so much less frequently than birds of similar size that bring food in the bill or mouth.

It is hardly possible to see what food the parent hummingbird passes to her nestlings as she regurgitates with her bill inserted deeply into their throats. A Rufous-tail that I watched collected minute creatures and visited flowers before coming to feed her young, from which I inferred that they received both insects and nectar. The rapidly delivered food enters an oesophageal pouch that forms a prominent, dark swelling on the right side of the nestling's neck—as in passerine nestlings, such as seedeaters and Bananaquits, that are fed by regurgitation.

Brooding.—On the bright, sunny morning of 7 July the two nestlings that I watched, then three and four days old, were brooded 20 times in six hours, for intervals that ranged from a fraction of a minute to 12 minutes and averaged 5.5 minutes. The parent's 20 absences lasted 3 to 39 minutes and averaged 11.9 minutes. She warmed her nestlings for 31 per cent of the six hours. Sometimes, when she brooded without first feeding, the parent flew up from one side and, without a break in her movement, turned around to settle on the nest facing the same side—a surprising feat. While sitting

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she sometimes voiced a rapid series of slight, sharp notes, a sort of buzz or rattle. Six days later, when these nestlings were nine and 10 days old, they were left uncovered throughout the morning. The same was true on the next morning that I watched, when they were 15 and 16 days old.

Even nocturnal brooding usually ceases when the nestlings are six or seven days old and still nearly naked. At one exceptional nest the parent brooded until her nestlings were nine days old. This unusually prolonged nocturnal brooding may have been caused by the presence of a Silver-throated Tanager (*Tangara icterocephala*) that roosted only 30 cm from the nest in a *Palicourea* shrub, its bright yellow breast turned toward it; the hummingbird might have occupied the nest to protect her young from the harmless tanager. But for at least three more nights the tanager slept in the same spot while the parent hummingbird was absent. Such early cessation of nocturnal brooding is usual in hummingbirds, especially at lower altitudes. While sleeping on the nest the adult keeps her head exposed, with the bill projecting forward and tilted slightly upward, as hummingbirds do while roosting in a tree. While they sleep on the nest one can touch them in the beam of a flashlight.

Although Rufous-tailed parents leave their nestlings exposed, even on a rainy night, after they are a week old, they shield them from strong sunshine until they are considerably older. Late on a sunny morning I found a parent brooding nestlings, then 12 and 13 days old, that she had failed to protect from hard rain several days earlier. Another parent tried to shield nestlings seven and eight days old from strong sunshine by sitting on the nest's rim with spread wings, but she was not well placed and the young continued to pant with open bills.

Sanitation of the nest.—During the nestlings' first few days the parent throws out droppings with the tip of her bill, as in other hummingbirds. After cleaning the nest she often sticks out her long white tongue. Older nestlings keep their nest clean by rising up to shoot their excrement beyond the rim.

Hardiness.—Nestling hummingbirds are amazingly tough and able to endure extremes that would be fatal to passerine nestlings of the same age. I was strongly impressed by their hardihood at the first nest which I watched, that in the ramie plant in front of my window near Almirante. After the young in this nest were devoured by fire ants, it remained deserted for six weeks. Then the parent returned, added bits of grass to build up the rim of the badly weathered structure, and attached fresh lichens to the outside. Before completing repairs she laid two eggs on the hard, impacted bottom, then continued to refurbish the old nest while she incubated, until it appeared as sound and comfortable as when new. But, weakened by many rains, it failed to withstand the pressure of the nestlings' growing bodies.

One afternoon I looked up from my microscope in time to witness a lively scene. A side of this nest had fallen away, dropping one eight-day-old nestling to the ground while the other clung with its feet to the remnant,

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struggling desperately to climb back by hooking its short bill over it. Their excited mother hovered around, holding a tuft of down in her bill. I watched until the squirming youngster dangled precariously by one foot, then rushed out to rescue it, and to pick the other from the ground; while their mother retired to an electric wire overhead and continued her distressed chittering.

From a disc of heavy paper I fashioned a shallow cone, which I attached to the ramie as near the position of the fallen nest as I could, then lined it with soft cotton and laid the nestlings in it, apparently none the worse for their experience. The parent continued to feed them in the improvised nest but no longer brooded them.

A one-meter fall and the handling necessary to rescue them were not the only tribulations that these tiny and apparently so delicate nestlings survived. Even before the collapse of their nest some of the leaves that had shaded them withered and dropped, exposing the naked nestlings to the full intensity of tropical sunshine. They sat with necks stretched upward, mouths widely gaping, and glassy, staring eyes. Although their mother tried to shade them, her shadow did not always fall upon them. She herself was panting in the brilliant sunshine. Even when she brooded, to protect them from intense insolation rather than to warm them, a nestling pushed its head out between her body and a wing and continued to gasp with open mouth.

The next ordeal of these nestlings was a rainstorm that continued for 24 hours, including intervals of intense tropical downpours. Their mother had ceased to cover them and the scant remaining foliage of the ramie plant afforded slight shelter. After a nightlong rain I watched them through much of a dreary day. In the heaviest downpours the two-week-old nestlings sat in their improvised nest with eyes closed and bills pointing straight up, shaking their heads from side to side when struck by a particularly large drop. Their expanding plumage gave little comfort, and the cool rain soaked them to the skin.

At intervals between the hardest showers their faithful mother came, her dark bill dusted with white pollen from the banana flowers, perched on the rim of the paper cup, and fed her wet offspring. Often one or both of the nestlings refused nourishment. Then she gently touched the inert nestling's bill once or twice with hers, as though to stimulate it to raise its open mouth and be fed; but often it was too wet and miserable to respond. At each visit she ran over the nestlings' plumage or part of the nest with her tongue, an act I never saw in dry weather. From the way her throat worked I concluded that she was sucking up some of the excess water, much as I have watched *Polistes* wasps remove droplets from their combs. With such devoted maternal care the half-grown nestlings survived the rainstorm. In similar circumstances passerine nestlings much larger and better feathered than these hummingbirds have been brooded much, lest they succumb.

An equally impressive demonstration of the hardihood of Rufous-tail nestlings was given by a brood in a shrub in front of our house. The

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time was late October and early November, the height of the rainy season when scarcely any birds except hummingbirds were nesting; the place was the Costa Rican foothills at an altitude of 750 m, where rains are colder than at sea level in Panama where the nest in the ramie was situated. After prolonged, torrential rain on the afternoon of 25 October, these nestlings were, unaccountably, left uncovered through the drizzly night that followed, although they were then only five and six days old, their eyes still closed, and their black skins naked except for the few tiny tufts of natal down along the middle of their backs. Yet after their long night's exposure they gave no sign of having suffered. Their mother brooded much during the afternoon deluges that followed, and continued to cover them as the rainy evening passed into the rainy night. This was the last time that I found the parent sitting on the nest, except to shield the nestlings from strong sunshine. They were left exposed to all the downpours that followed during that wet October and November. After hours of drenching rain on the afternoon of 28 October I visited the still nearly naked nestlings in the night. Although quite cold to the touch they rose up with gaping mouths, begging for food, in the beam of my flashlight. Next morning they appeared to be in good health. They lived to fly from the nest.

As we have seen, the female hummingbird molds her nest snugly around her own body so that while incubating she fills the top of the cup like a cork in a bottle. Before the two nestlings fly they approach their mother's size and, naturally, the nest becomes too small for them. One may rest above its sibling. The downy structure yields to the pressure of their growing bodies and its originally incurved walls flare outward. Especially in wet weather, they may flatten the nest to a platform on which the now feathered nestlings continue to rest, if they do not fall to the ground, as I have seen happen. The nest is so firmly bound by cobweb to its supports that it does not readily fall. However, if one of its supports becomes detached from the plant, as happened to the petiole of the ramie leaf on which the nest in Panama was built, or if the nest breaks loose from one of its supports, it pivots around to the lower side of the remaining support and hangs there, opening sideways. Small nestlings probably tumble out, but a feathered nestling may cling to its hanging nest with its body upright.

The nesting habits of *Amazilia* and other hummingbirds that build similar nests appear to fall short of perfection, or to be a compromise between several factors. The tiny nest is less likely to attract hostile eyes than a bigger one, and by fitting snugly into it the parent warms the eggs more effectively; but it provides inadequate accommodation for older nestlings. By ceasing to brood by night while the nestlings are still naked the parent reduces the risk of being captured along with her young by a nocturnal predator; but by leaving them exposed she probably retards their development, which is much slower than that of much larger passerines. Her failure to shield nestlings from rain is a more surprising negligence; but perhaps, without a male's help, she cannot spare enough time from foraging for herself and offspring in inclement weather. To compensate for these seeming

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deficiencies in the hummingbirds' nesting habits, the nestlings are amazingly resistant for homeothermal young. Hermit hummingbirds, which fasten their nests beneath sheltering leaves, spare their nestlings some of the stresses to which nestling Rufous-tails are exposed.

Nestling Period.—The nestling period of Rufous-tailed Hummingbirds is quite variable. If disturbed, or if their nest flattens or is otherwise damaged, they may fly away, well feathered, when 19 or 20 days old. The periods reported in my earlier paper (1931) for eight young raised near sea level in Panama and Honduras, 18, 19, 19, 19, 19, 20, 21, and 22 days, were probably slightly too short for these several reasons. I have also recorded nestling periods of 19 and 20 days for two young at 750 m in Costa Rica, whose nest developed a hole. Weather strongly influences the nestling period. Two young in the same locality in Costa Rica, hatched at the end of January and raised in the warm, dry month of February, left spontaneously when only 20 and 21 days old. Here two young raised in December and January abandoned their nest at 23 and 23 days of age; two in rainy August at 25 and 26 days; while those reared beneath the cold deluges of October and November, as already told, stayed in their usually sodden nest until 25 and 27.25 days of age. As far as I know, none of these Costa Rican nestlings had been disturbed in any way. Taking all these data together, the average age at which 18 young left the nest was 21.5 days; the range 18 to 27.25 days.

The young leave the nest in either forenoon or afternoon. Already they fly very well, thanks to the vigorous wing exercises while still in the nest. They resemble adults but the feathers of back and rump have brownish tips, which make the plumage appear rough, and breast and sides are tinged with cinnamon. Their bills and tails are still not fully grown.

NESTING SUCCESS

In 16 nests of known outcome, found in El General before the eggs hatched, 32 eggs were laid. Nineteen of these eggs hatched, and 11 young fledged from six nests. Accordingly, 37.5 per cent of the nests yielded at least one fledgling, and 34.4 per cent of the eggs yielded fledglings. From a nest in an orange tree the eggs were apparently knocked out by a falling orange, and incubation was not resumed after the egg that remained intact was replaced. Other causes of loss are unknown.

In the same locality where these records were made, the equally abundant Scaly-breasted Hummingbird (*Phaeochroa cuvierii*), which also builds an open cup nest in isolated or semi-isolated trees and shrubs, usually somewhat higher than those of the Rufous-tail, has nested with greater success. In 19 nests of known outcome found before hatching, 37 eggs were laid. Twenty-six of these eggs hatched and 18 young lived to fly from 10 nests. Thus, 52.6 per cent of the nests produced at least one fledgling, and 48.6 per cent of the eggs yielded fledglings—a very good record.

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It is of interest to compare these figures for the success of open nests in trees and shrubs with those for four species of hummingbirds—Band-tailed Barbthroat (*Threnetes ruckeri*), Bronzy Hermit (*Glaucis aenea*), Long-tailed Hermit (*Phaethornis superciliosus*), and Little Hermit—that fasten their nests beneath strips of banana leaves, where they appear to be inaccessible to all vertebrates unable to fly. These birds were in a small banana plantation surrounded by woods also on the farm in El General where Rufous-tailed Hummingbirds were chiefly studied. Here 45 per cent of 33 nests yielded at least one fledgling and 41 per cent of their 66 eggs produced flying young. Again, the causes of loss were largely unknown, but bats were the suspected predators.

At Almirante from December 1928 to June 1929 Rufous-tailed Hummingbirds nested less successfully than in El General. Of 17 nests started 13 received a total of 24 eggs. Eleven of these eggs hatched, but only six young fledged from three nests. Only 23.1 per cent of the nests in which eggs were laid produced fledglings, and only 25 per cent of the eggs did. Breeding success would have been much lower if I had not rescued and returned to their nests four of the six young that survived to fly. In El General none of the young that fledged owed their lives to my intervention.

At Almirante one set of eggs was abandoned, probably in consequence of human disturbance, and one brood of two was devoured by fire ants before they were feathered, but most of the losses were attributable to the destruction of nests by other Rufous-tails, that tore material from them for incorporation in their own structures. Among the ornamental plants surrounding the house and little laboratory, nests of Rufous-tails—the only hummingbirds that I found breeding—were surprisingly abundant. Of the 63 nests that I have recorded in half a century, 17 were found here in only six months, some of them separated by 30 m or less. However, at that time down for lining these nests appeared to be scarce, so that some hummingbirds laid in nests composed of fragments of grass and weeds, with a few bits of moss or lichens on the outside, but so devoid of a downy lining that the eggs touched the supporting branch. The lining was added later, as opportunity arose. The best source of seed down was the balsa trees (*Ochroma* sp.) growing along the neighboring lagoon; but they were several hundred yards distant and, moreover, their long, prismatic pods did not split to release masses of the resilient, silky down, in which the seeds were embedded, until late in the period in which my observations were made. To remedy the deficiency the Rufous-tails stole material from each other's nests, not sparing those with eggs if they found the owner absent. Sometimes a nest was torn apart by hummingbirds that carried their booty in different directions, indicating that more than one individual was engaged in plundering it. Nowhere else have I known hummingbirds of any kind to tear apart occupied nests, not even where two were close together like some nests of Violet-headed Hummingbirds and Little Hermits that I have seen.

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BEHAVIOR OF A FRUSTRATED BUILDER

I gave much attention to one of the Rufous-tailed victims of her neighbors' theft, who was not herself guiltless of the same habit. She tried to build in a gnarled, spreading, old cashew tree in a corner of the garden, and in an avocado tree growing close beside it. She would collect a little material in her chosen site, only to have it vanish, often the same day, carried off by other Rufous-tails, or sometimes by a Black-fronted Tody-Flycatcher (*Todirostrum cinereum*), to line the pensile nest it was building in a nearby *Codiaeum* shrub.

One Rufous-tail acted with stealth that surprised me in a hummingbird, and suggested little-suspected mental qualities. Intent upon theft the hummingbird flew into the cashew tree while the builder was plucking a lichen from the bark of the neighboring avocado tree, in plain view. Instead of going straight to the incipient nest that she would pillage, the newcomer perched on a low twig of the cashew tree, so inconspicuously that the builder apparently failed to notice the intruder when she returned to fasten the lichen to her nest. No sooner had the unsuspecting builder finished her task and flown beyond sight than the thief advanced, hovered beside the little pile, tore a large billful of down from it, and carried it away. When the nest's owner returned she continued her fruitless building as though nothing had gone amiss.

For at least 31 days this long-suffering hummingbird, which appeared to be inexperienced in the art of building, continued her efforts to complete a nest. She changed her building site eight times, alternating between four different locations, two in the cashew tree and two in the avocado. She made at least 12 fresh beginnings, each of which was more or less completely obliterated. When she laid an egg, it fell to the ground because she still had no cup to hold it.

As the weeks passed, this hummingbird's increasingly disorganized behavior suggested bewilderment, distress, or mental derangement. Often with empty bill she returned to the barren crotch where she had been building and went through all the motions of shaping to her body materials that were not there. Sometimes after adding a bit of material she started to fly off, only to turn around and sit in her site again. She might do this half a dozen times in quick succession, as though fearing to leave her nest unguarded. One morning she appeared unable to decide in which of two empty sites in the avocado tree to build, for she went through the motions of shaping a nest in one, then in the other on the opposite side of the tree, then back again to the first. After several such alternations she settled on one, where she continued to build for the remainder of the day. Her efforts to fashion a nest became increasingly lax, her successive attempts formless masses of the usual constituents. Likewise, defensive behavior waned and she permitted birds of several kinds to rest near her nest. Toward the end of March she abandoned her attempts to complete a nest in the cashew tree. I marvelled that, after so many frustrations, she had not sooner

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gone elsewhere to build; but the hummingbird's attachment to a chosen locality is strong.

REPLACEMENT NESTS

The high rate of nest destruction at Almirante caused repeated nestings by the same individual. Although these hummingbirds were not marked, in two instances the new nest was so near one that had just been destroyed, and in a similar site, that I was confident that it belonged to the same bird. On 4 February the eggs disappeared from a nest in a citrus tree, and on 13 February the first egg was laid in a flimsy, unfinished nest similarly situated in a neighboring citrus tree. On 14 April a week-old nestling and an unhatched egg vanished from a nest on a slender, drooping spray of a timber bamboo, and on 21 April the first egg was laid in a new nest that had been built close beside the remains of the earlier one. Thus, *Amazilia tzacatl* may lay again in a new nest only seven to nine days after the loss of eggs or nestlings.

YOUNG AFTER LEAVING THE NEST

From the nest in the shrub in front of our house, where the nestlings endured such hard drenchings from November's downpours, the first left early in the afternoon of the thirteenth, aged 25 days, and the second flew between 12:00 and 14:00 on the sixteenth, aged 27 days (assuming that they departed in the order that they hatched). On the morning of 7 December I twice saw the parent feed a fledgling in a rose-apple tree, about 15 meters from the nest. Between meals the juvenile probed a rose-apple flower and also calyces from which petals and stamens had fallen, sometimes while clinging to the sepals. It also made longer excursions.

During the next 10 days I repeatedly saw this young hummingbird or its sibling receive food in various trees near their nest. On two mornings I witnessed three feedings in the hour from 7:00 to 8:00. While the parent's bill was only slightly inserted into the recipient's mouth, I occasionally saw objects that appeared to be tiny insects or spiders pass to the young bird. Feedings were always brief. On the afternoon of 17 December a juvenile received at least four meals on the low branch of a reina de la noche shrub (*Datura arborea*) near the nest site, the last two at 16:39 and 16:51. Between meals the young Rufous-tail rested quietly on the dead branch much of the time, but it visited a neighboring patch of red lobelias, hovering expertly in front of many of the tubular flowers. It also appeared to catch insects on short darts into the air.

This was the last day on which I saw a parent feed a juvenile. On 22 December, in the area where all the feedings occurred, I repeatedly saw one Rufous-tail pursue another; but in flight it was no longer possible to distinguish adult from young. Depending upon whether it was the older or younger of the two juveniles, the one that I last saw receive a meal was then 58 or 59 days old, and had been out of the nest for 31 or 34

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days. In other hummingbirds that I have watched parental attendance has continued for similar periods: to the ages of at least 65 and 52 days in the Scaly-breasted Hummingbird (*Phaeochroa cuvierii*), to 56 days in the Band-tailed Barbthroat (*Threnetes ruckeri*), to 48 days in the Long-billed Starthroat (*Heliomaster longirostris*), and to 40 days in the White-eared Hummingbird (*Hylocharis leucotis*) (Skutch, 1972).

SUMMARY

In rainier regions from northeastern Mexico to southwestern Ecuador, the Rufous-tailed Hummingbird is often the most conspicuously abundant hummingbird in gardens, plantations, and other cleared areas with abundant flowers. From the lowlands it ranges upward to 1,500 or 1,825 m. It enters light woods and even more open parts of rain forests to visit flowers, but it has not been found nesting in woodland.

It sucks nectar from a great variety of flowers and catches tiny insects in the air. Individuals defend profusely blooming plants from other hummingbirds, large bees, and butterflies. This exclusiveness differs in several ways from typical territorial behavior.

Rufous-tails bathe by wetting their plumage on drop-laden leaves and saturated cushions of moss, or by dipping into water-filled tanks of bromeliads.

Males gather in singing assemblies where, through most of the year except at the height of the dry season, they tirelessly repeat quaint little notes from early dawn to around sunrise, seldom later.

Sixty-three nests, from localities ranging from northern Guatemala to the Andes of western Venezuela, were built in a great variety of plants in open situations, at heights ranging from 1 to 6 m; about half were 1.5 to 2.5 m up. Building, by the female only, is described.

In the Valley of El General eggs have been found in all months except February, March, April, and September, but most sets are laid in December. In the more uniformly rainy Caribbean lowlands of Central America, nesting continues throughout the year but appears to be at its height in the very months when nests have not been found in El General.

The two eggs of the usual set are laid early on alternate days, incubated by the female only, and hatch in 15.5 days to 16 days and a few hours.

The development of nestlings is described. The female feeds them by regurgitation, usually both on a single visit, at rates which vary from 0.75 times per nestling/hour when they are a few days old to 1.2 times when they are feathered.

From the first the nestlings are amazingly hardy, enduring exposure to prolonged rain and direct sunshine, and falls that would be fatal to many passerines that are much bigger. Even nocturnal brooding usually ceases when they are six or seven days old and still nearly naked. The parent shields them from sunshine after she has ceased to cover them in rain. The nests, too small to accommodate older nestlings, often burst asunder or collapse, especially in wet weather.

FORK-TAILED WOODNYMPH

The average age at which 18 young left their nests was 21.5 days, with a range of 18 to 27.25 days. Eighteen-day-old young probably left because of disturbance or nest collapse, but they flew well. The longest nestling period was recorded in very rainy weather.

Of 16 nests in the Valley of El General, 37.5 per cent yielded at least one fledgling and 34.4 per cent of 32 eggs produced flying young. This is compared with the breeding success of certain other hummingbirds.

The much lower breeding success of an unusually dense population in a garden near Almirante, Panama was caused chiefly by the destruction of nests by Rufous-tails tearing apart nests of other Rufous-tails to procure materials for their own nests. Such behavior, evidently resulting from a local shortage of plant down, has not been observed elsewhere.

For at least 31 days a female tried vainly to build a nest, frustrated by the depredations of her neighbors. Her behavior became increasingly disorganized and ineffective.

Females may lay again, in a new nest, seven to nine days after the loss of eggs or nestlings.

One parent continued to feed juveniles for over a month after they left the nest, or until they were at least 58 days old.

FORK-TAILED WOODNYMPH

Thalurania furcata

The Fork-tailed Woodnymph is a highly variable hummingbird with an immense range extending from western Mexico to northern Argentina and to Ecuador west of the Andes. The soundness of its classification is disputed by some authors, who treat the population in Central America as a separate species, *T. colombica*, the Crowned, or Blue-crowned, Woodnymph. Whatever the correct name may be, the males of the woodnymphs of Costa Rica and Panama, as far east as the Canal Zone, with which this account deals, are middle-sized hummingbirds, about 11 cm long, with nearly straight black bills of moderate length and fairly long, deeply forked tails. The forehead and front of the crown are bluish violet or royal purple; hindhead greenish; upper back and shoulders more or less intense violet-blue; lower back and rump metallic bluish green; tail blue-black or violaceous. Below the glittering emerald green of the throat and chest has a convex posterior outline and contrasts sharply with the rich violet-blue of the lower breast and abdomen. The female has a shorter, slightly indented tail, with the two outer feathers tipped with dull white or gray. Above she is metallic green. Below she is pale gray where the male is green, and much deeper gray, more or less tinged with green, where the male is violet-blue—a pattern that suggests her relationship to the intensely colored male and provides the best recognition mark of this plainly attired female.

In southern Central America the Fork-tailed Woodnymph inhabits humid

FORK-TAILED WOODNYMPH

forests of the Tropical Zone, extending upward to about 1,200 m in Costa Rica and western Panama. Usually it is noticed in the lower levels of woodland, where its neighbors are the much duller hermit hummingbirds, chiefly species of *Phaethornis*; but flowers rich in nectar may attract it to the treetops, and even into neighboring sunny clearings, where it seldom remains after its meal is finished. It is a solitary, silent bird about which we have much to learn. In many years amid forests where it is not rare, I have discovered nothing about its courtship. I have never heard a male singing from a perch, alone or in an assembly, as many woodland hummingbirds do, nor have I seen one display on the wing before a female, and I have gleaned no information on this subject from the literature or directly from other ornithologists.

In the shrunken forests of the Valley of El General, the small, tubular white flowers, massed between two large, red bracts, of the tall rubiaceous shrub *Cephaelis elata* provide much nectar for Fork-tailed Woodnymphs. Great-leaved wild plantains of the genus *Heliconia* are also an important source of nourishment. When, in the middle of the wet season, trees of the cerillo (*Symphonia globulifera*) display a profusion of flowers that resemble red cherries, woodnymphs rise to the treetops to share their nectar with more numerous Brown Violet-ears (*Colibri delphinae*) and White-necked Jacobins (*Florisuga mellivora*). Woodnymphs also visit the epiphytic orchid *Elleanthus capitatus* to draw nectar from the small pink flowers, which protrude in a circle from the clear, colorless jelly that envelopes the massive hemispheric inflorescence. The tiny blue or purple flowers of *Stachytarpheta* spp., introduced shrubs of the verbena family, entice woodnymphs into the sunshine from nearby forests.

Once, standing beside a forest rivulet, I watched a male woodnymph bathe in a still, clear pool. After hovering a foot or less above the surface, he would suddenly drop until his body was half submerged. He remained in the water only an instant, then rose to an overhanging slender twig, where he shook the drops from his glistening plumage, and preened his feathers with his long bill. Again and again he dipped lightly into the limpid water.

NESTING

I have seen only five nests of the woodnymph, two on Barro Colorado Island in the Panama Canal Zone and three at Los Cusingos. All were in the forest, four from 1 to 2 m up and the fifth 4 m above the ground. Each rested upon a slender horizontal branch or petiole of a shrub or sapling, at a point where one or more twigs provided lateral support. These nests were tiny, compact cups, with incurving walls that made it more difficult for the eggs to roll out. The two on Barro Colorado were composed largely of light-colored vegetable down, whereas brown scales from the fronds of tree ferns were the main components of those at Los Cusingos. All were more or less covered with gray or gray-green lichens, and those at Los

FORK-TAILED WOODNYMPH

Cusingos had green moss attached to the outside or hanging below. Cobweb bound the materials together. Each of the two nests on Barro Colorado held two white eggs in March 1935. One of the nests at Los Cusingos had two eggs on 14 February 1976. Another held, on 25 February 1943, a single egg that soon vanished. The third contained two eggs on 30 May 1953. Thus, the woodnymph appears to nest chiefly in the dry season but continues into the rainy months. At all of these nests I saw only females. In three or possibly four of the nests the eggs hatched, but in none did the young live to fly.

SUMMARY

The Fork-tailed Woodnymph inhabits humid forests of the Tropical Zone, where it seeks nectar chiefly in the underwood but may rise to flowering treetops or enter neighboring clearings rich in bloom. It is a solitary, silent bird about whose courtship nothing appears to be known. It bathes by dipping on wing into forest pools.

Five nests, found at heights of 1 to 4 m in the forests of southern Costa Rica and Panama, were downy open cups, which held eggs from February to May. Only females were seen at these nests. None was successful.



FIG. 3. Violaceous Trogon, *Trogon violaceus*.

Family TROGONIDAE
VIOLACEOUS TROGON

Trogon violaceus

In an earlier account of this widespread, small, yellow-bellied Trogon (Skutch, 1972), I told how the male and female take turns digging into a large, turbinate, silvery gray wasps' nest, hanging high in a tree. They prefer occupied nests, and alternate between catching the stinging wasps on aerial darts and excavating a chamber in the vespiary. Then they lay their eggs and rear their young amid the brood combs, which have been abandoned by the wasps. In the Valley of El General all the nests of the Violaceous Trogon that I have seen, 10 in number, were in vespiaries of similar shape, although apparently not always made by the same species of wasps. Beyond this valley I had found only one record of Violaceous Trogons digging into vespiaries, evidently to make a nest chamber: Wetmore (1968) reported that "near Almirante one pair had made an opening in the upper end of a huge wasp's nest 20 meters from the ground in an open-limbed tree." Almirante is on the Caribbean coast of Panama near the Costa Rican border. Elsewhere, as on Barro Colorado Island in the Canal Zone, Violaceous Trogons had been found nesting in cavities in decaying stumps and in termitaries, as do a number of other species of trogons (Eisenmann, 1952). From the more northerly parts of the Violaceous Trogon's range, no records of nests were available to me. Accordingly, in 1972 these trogons were known to occupy vespiaries only in a rather limited area comprising southern Costa Rica and an adjacent part of Panama. And, apparently, no other kind of trogon shared this surprising habit.

On 18 February 1978 while riding in a bus with a group of birding tourists along the road from Flores and Santa Elena to Sayaxche in El Petén, Guatemala, we found two pairs of Violaceous Trogons excavating large, turbinate wasps' nests with silver-gray, papery envelopes. The first was about 15 m up in a big ceiba tree near the road. The second, a few kilometers farther along, was about 8 m up, directly above this unpaved but moderately busy highway. In both cases the trogons, apparently well accustomed to traffic, permitted us to watch them at their work. These discoveries show that Violaceous Trogons' use of vespiaries is by no means a local habit but spread over a wide range. Just how widespread it is remains to be seen.

While watching birds with Eugene Eisenmann and Jaime J. Pujals along the Achiote Road on the western side of the Canal Zone, on 25 March 1974, we found a pair of Violaceous Trogons apparently preparing to nest in a site as unexpected as an occupied vespiary. On a thick, ascending, epiphyte-burdened branch of a big tree standing on the bank above the roadside, in open woodland with scattered large trees, grew a vigorous plant of *Polypodium crassifolium* or some closely similar fern. The roots of

VIOLACEOUS TROGON

this robust fern formed an irregular, compact, dark brown mass about 60 cm in diameter. Mixed with the roots was much decaying vegetable matter. The fern perched about 15 m above the bank.

The trogons had made a round opening low on the side of the root mass that faced into the woods, away from the road. Between 13:00 and 13:40, in bright, warm weather, the male and female went alternately to the hole, entering up to the base of the tail, which was pressed against the side of the mass and partly spread, revealing the white outer rectrices barred with black. We could not see what they did inside, but the shaking of the exposed parts of their bodies and wings suggested that they were vigorously tearing away the roots. When, after a long spell of work, the female flew out, much loose material followed her and fell to the ground. While at the root mass the trogons called a little in subdued voices.

We were unable to follow developments at this spot, but in a letter dated 22 July 1974 Dr. Pujals reported that a few days earlier he had, in different localities, found two pairs of Violaceous Trogons definitely nesting inside root masses of epiphytes. With a degree of adaptability rare among trogons, the Violaceous has not only demonstrated its ability to live in areas where man has left only scattered trees, but also to carve its nest chambers in four quite different media: vespiaries, termitaries, decaying trunks, and large, compact masses of aerial roots. As far as I know, other trogons use only termitaries and trunks.

SELECTION OF NEST SITE

Over the years I had gathered evidence that male trogons of several species take the initiative in selecting nest sites and carving nests, but my most convincing example of this was provided by a Violaceous Trogon in 1972. Beginning early in the year a male, that apparently lacked a mate, called much in and around the riverside pasture in front of our home in the Valley of El General. Here, in the preceding year, wasps had built a turbinate nest in the top of an old, dying guava tree. In early April I discovered that the wasps had abandoned this vespiary. Later, in the side of this structure I noticed a small depression, which was slowly enlarged. From time to time the male trogon came to this tree and called persistently, either with the mellow *cow cow cow* . . . or with lower, softer notes. Although he evidently made the hole in the vespiary, several weeks passed before I found him at work, or with a mate.

Soon after noon on 3 May I heard the male trogon delivering his softer, more murmurous notes, which he continued so long that I went to investigate. Finally, at 13:51 he clung in the gap that he had made in the vespiary, with his head inside and the rest of his body exposed. For six minutes he remained in this position, apparently tearing at the brood combs. While he was so engaged I noticed a female perching nearby—the first time I saw one in the vicinity. Thrice more the male went to the vespiary, each time remaining there only a minute or two, while the female rested on nearby twigs. During his fourth spell of work at the wasps' nest she flew

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away, without having gone to it. The male stayed in the tree, softly murmuring almost without pause but not going again to the vespiary until 14:15. Then he fell silent and flew northward.

At 11:30 the following day, low notes constantly repeated again drew my attention to the guava tree, where I found a female Violaceous Trogon, but no male. She called much, and once clung for several minutes in the hole in the side of the vespiary; but she did little, if any, work there. When, after nearly half an hour, no male appeared, she flew away. Early the next afternoon, 5 May, the male called from the very top of the guava tree but no female was in sight, and he did not go to the vespiary while I watched. These trogons wandered, often singly, over a wide area and seemed to have difficulty coordinating their activities.

Late in the morning of 7 May both sexes were present, and for the first time I saw the female apparently working at the nest, with the anterior half of her body inside the cavity. On 9 May the two trogons took turns at the vespiary, first the male for five or six minutes, then the female for 11 minutes, then the male for eight minutes. His spell ended when a branch, falling noisily from a nearby tree, frightened him out of the excavation. This had deepened during the last few days so that the trogons now entered as far as the tips of their wings. Soon the female flew away and, after calling softly for a while, the male followed.

This was the last time that I saw the female in the dying guava tree. For the next 10 days the male continued to visit it, usually late in the morning or around noon. He called softly and sometimes went to the vespiary, clinging in front and occasionally entering the excavation, without, as far as I could learn, continuing to enlarge it. Probably the female abandoned the vespiary because it was somewhat smaller than those in which Violaceous Trogons usually nest; because it had become dilapidated after its desertion by the wasps; or because it was more closely surrounded by twigs and, accordingly, more accessible to snakes and other flightless predators than the exposed vespiaries that Violaceous Trogons usually select. Before the end of May this wasps' nest was torn from its support and vanished.

These observations suggest that a male Violaceous Trogon, still unmated, chooses a nest site, then tries to persuade a female to join him. If, after testing the site, she finds it unsatisfactory, she abandons it and him. The pair does not seek another site together, as constantly mated birds do. All that I have seen of trogons leads me to conclude that, when not held together by the shared tasks of rearing a brood, they are essentially solitary, although a number may congregate at a generously fruiting tree.

At La Selva in the Sarapiquí lowlands of Costa Rica, on 12 May 1967 I watched a Rufous Mourner (*Rhytipterna holerythra*) closely pursue a male Violaceous Trogon that had just caught an insect, making him drop his food. The mourner darted after the falling insect, but I did not see whether the bird caught it. This was the only occasion when I saw a passerine, or any woodland bird, practice this kind of piracy, which is not rare among marine birds.

VIOLACEOUS TROGON

SUMMARY

The Violaceous Trogon's habit of capturing occupied wasps' nests and, after eliminating the wasps, carving a nest chamber and laying eggs among the brood combs, was first reported from the Valley of El General in Costa Rica. The more recent discovery of two pairs digging into vespiaries in northern Guatemala, and one pair doing so in extreme western Panama, greatly extends the known range of this peculiar habit.

These trogons also hollow out nest chambers in large, compact root masses of epiphytic plants, as well as in termitaries and decaying trunks.

The male selects a nest site and tries to attract a mate. After weeks of calling one male enticed a female to a vespiary in which he had barely begun a nest cavity. She dug a little at it, evidently found the site unsatisfactory, and went elsewhere. For 10 more days he tried vainly to interest a female in his vespiary, then abandoned it.

A Rufous Mourner pursued a male Violaceous Trogon until he dropped the insect he had just caught.





FIG. 4. Rufous-winged Woodpecker, *Piculus simplex*.

Family PICIDAE

RUFIOUS-WINGED WOODPECKER

Piculus simplex

The Rufous-winged is a small, beautiful woodpecker about 18 cm long. The male's head and hindneck are bright red, with a patch of olive-green on each side from below the eyes to the ear coverts. His back, rump, and wing coverts are golden olive-green. When spread in flight his wings reveal much cinnamon-rufous, barred with black on the outer surface of the remiges, plain on the underwing coverts. His chin and throat are olive, unmarked; upper breast greenish olive with buffy spots; and the remaining underparts buffy yellow narrowly barred with dark olive. His tail is black and olive-green. His eyes are dull yellow; upper mandible blackish with a prominent pale streak along the cutting edge at the base; lower mandible whitish, darkening toward the tip; legs and toes dark. The female has only the nape and hindneck red, the remainder of her head being yellowish olive, and her eyes are brown. Otherwise, she resembles the male.

The Rufous-winged Woodpecker ranges through humid lowland forests from the Caribbean coast of Honduras to southern Costa Rica and possibly western Panama, where it has not been recorded since the 1920's (Ridgley, 1976). It is found chiefly at altitudes below 600 m. It was fairly abundant in the wet forests between the Golfo Dulce and the Río Grande de Térraba in 1947, but I did not meet it in the Valley of El General until 1950, 15 years after I began to study birds in this region. Since that date it has resided and nested in our forest at Los Cusingos, at 750 m, the highest point at which I have seen it. The habitat of this woodpecker is shrinking with the destruction of forests.

These woodpeckers roam widely through the rain forests, alone or in mixed flocks of small birds. Rarely they extend their excursions into neighboring clearings with scattered trees. Although others have recorded them near the ground, nearly always I have found them well up in the trees, at mid-height of the forest or higher. I have not seen them dig deeply into wood for food. Much of their foraging is done on slender branches rather than on thick trunks. They peck into rotting limbs and decaying spots in sound ones, especially knot holes, and investigate patches of moss, sometimes prying off pieces, much as woodcreepers do. Sometimes they probe between branches and the roots of epiphytes attached to them. On thin dead twigs, hardly thicker than those that a piculet might exploit, they act much like these pygmy woodpeckers, clinging in any attitude, sometimes beneath a twig, without using the tail for support. Here they peck in rather deeply and appear to extract food from the center. Restless birds, they rarely work long at one spot but may remain long in a wide-spreading tree, moving from branch to branch. The objects of their search are nearly always too small to be seen from the ground, but I suspect

RUFOUS-WINGED WOODPECKER

that they find chiefly ants. Like many ant-eating woodpeckers, they feed their young by regurgitation.

VOICE AND MECHANICAL SOUNDS

The call of this woodpecker is high, sharp, and nasal, with a peculiar twang that makes it unmistakable. No other woodpecker that I know has such a whine. It also beats rapid, long-continued tattoos. One morning in mid-February I watched a Rufous-winged Woodpecker cling high in a dead tree that towered above a second-growth thicket near woodland. Again and again it drummed upon the broken-off end of a stout branch, 18 or 20 m up. Between tattoos it called loudly in its penetrating voice, sometimes as many as six times in rapid succession. For about a quarter of an hour it continued to drum and to call alternately, making itself conspicuous from afar. During the following days these woodpeckers continued to be noisy. A female pecked at the side of a tall, slender dead trunk, as though testing its suitability for a nest hole. For about ten minutes she clung there, hammering at the trunk, calling loudly, and preening. Later she behaved in the same way on a lower dead trunk. She was evidently trying to attract her mate (which I had seen with her not long before this) to a nest site, but he did not respond. None of these dead trees was used for nesting.

NEST BUILDING

On 1 March 1972 sounds of hammering drew my attention to a female Rufous-winged Woodpecker carving a hole 3.5 m up, on the lower side of a slightly leaning stub about 23 cm thick. The stub, far advanced in decay, stood in light second-growth woods, composed chiefly of tall trees of *Goethalsia meiantha*, on low, rocky ground beside the Río Peñas Blancas. She was clinging to the outside of the trunk, clutching the rim of a wide round doorway, and pushing her head and shoulders inside each time she delivered a blow or removed loose chips. In rapid succession she pulled out many billfuls of wood that she threw sideways with a slight flick of her head, or sometimes tossed over her head. After 21 minutes she called several times with nasal notes that promptly drew her mate. He clung beside her while the two repeatedly, and very rapidly, seized each other's bills. Between these "kisses" the female pecked at the rim of the orifice and appeared to feed her partner, although, as far as I saw, she had nothing to give him. After this greeting ceremony the female flew away and the male continued for the next 100 minutes to enlarge the hole. He was still at work when I left.

Bill-touching in courtship has been witnessed in the Ivory-billed Woodpecker (*Campephilus principalis*) by Tanner (1942) and the Crimson-crested Woodpecker (*Campephilus melanoleucos*) by Kilham (1972). Courtship feeding has rarely been recorded in the woodpecker family; but Short (1973) saw a male Olive-backed Woodpecker (*Dinopium rafflesii*), an Asian species,

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feed his partner as he replaced her at the cavity they were carving. Short (1974) also watched seven cases of courtship feeding by the Hispaniolan Woodpecker (*Melanerpes striatus*), in five of which the female fed the male, while in two the male delivered food to his mate, always by regurgitation. Likewise, he watched a Guadeloupe Woodpecker (*Melanerpes herminieri*) feed its mate at the nest.

On 2 March, the day after I found the Rufous-winged Woodpeckers starting their nest, I was unable to watch them, but I did throughout the forenoon of 3 March. The morning was sunny and dry, after three nearly rainless weeks. Although I arrived at 6:30, I neither saw nor heard a member of the pair until 7:52, when the male suddenly alighted on a neighboring trunk. Two minutes later he went to the hole, at which he worked rather steadily for the next 72 minutes. At first he carved from the outside, but soon he entered to throw out many billfuls of wood fragments. Apparently the cavity was still uncomfortably small, for he worked alternately inside and outside. As the hole grew deeper and he sank lower in it, he worked increasingly inside. In the midst of his work period the female silently alighted below the doorway. He flew out but promptly returned to cling beside her. Repeatedly they grasped bills, each time momentarily. After this ceremony the female flew away and the male resumed work inside the hole. In about a quarter of an hour she returned and apparently they touched bills through the doorway for a minute or two, although, since her back was toward me, I could not see this clearly. Then the male left and the female carved and threw out chips for the next three hours less three minutes. At 12:05 she flew away, thereby ending this day's work at the cavity, as I ascertained when I returned next morning and found no wood particles on leaves that I had spread below it before I left.

Periods of work were long. I next found the male at the hole at noon on 4 March, and he continued to toil in silence for the following 131 minutes while his mate remained out of sight. Between intervals of carving inside, where he was now invisible, he threw out debris in concentrated spells. Usually he did so from 15 to 30 times in rapid succession, but once 32, and once 43 times without intermission. In 131 minutes he ejected loosened wood 503 times, sometimes in overflowing billfuls, sometimes only one or two fragments. In a later work session of 80 minutes he tossed 164 billfuls from the doorway. Always, while one partner worked, the other was absent.

Carving continued for eight days after I found the recently begun hole. Months later when it appeared that it would not be used again, I pushed over the tottering stub, which was so rotten that it shattered when it struck the ground. Fortunately, the part that contained the cavity remained intact and I could measure what the woodpeckers had done. The vertical extent of their excavation was 40 cm. The diameter of their doorway was 57 mm. The cavity extended 32 cm below and 25 mm above this orifice. It was widest at the top, where it measured 12 by 10 cm in diameter. Narrowing downward, it was only 9 by 8 cm at 25 mm above the bottom. Everywhere it was wider from side to side than from front to back.

RUFOUS-WINGED WOODPECKER

EGGS AND INCUBATION

An egg was present in this cavity on 10 March, but by the following afternoon it had inexplicably vanished. By the afternoon of 14 March two more eggs had been laid. Like other woodpeckers' eggs they were white and glossy. They could not be removed for measurement without jeopardizing the nest.

During the incubation period my wife, son, and I watched through three full days, and I made numerous additional visits to learn which partner was in the nest, as could be done without causing the woodpeckers to leave. As in all woodpeckers for which we have information, except a few highly social species in which both sexes sleep in the nest, the male was alone with the eggs every night. Usually after waking he remained in the nest until his mate came to relieve him, which on four mornings she did at times ranging only from 7:37 to 7:50. Then she usually sat continuously for six or seven hours, until the male returned to incubate through the late afternoon and night. With, as a rule, only two changeovers each 24 hours, the pair followed the "ostrich pattern" of incubation (Skutch, 1976).

On 18 March when we made the first dawn-to-dusk vigil, the female replaced the male at 7:49 and sat continuously until he relieved her at 14:50, after which he remained in the nest until nightfall. On 22 March the female was in the hole continuously from 7:37 to 13:16, the male all the rest of the time from dawn until nightfall. On 21 March the pair departed from what appeared to be their normal routine. The male inexplicably flew out at 5:45 and did not re-enter the nest until 7:49, a minute before I saw the female. At 7:52 she replaced him. She had been in the nest only three hours and 25 minutes when her mate returned at the exceptionally early hour of 11:17 and sat until 15:05. At this hour the female came to begin a session which lasted until, at 16:26, he replaced her and remained until nightfall.

Changeovers were always unceremonious. When one partner flew up to the doorway the other nearly always left, then the newcomer entered. They neither called nor tapped, and at most they barely touched bills. On 21 March, when the male broke his usual routine by leaving at 5:45, he re-entered at 7:49, apparently in sight of his mate, which I first noticed a minute later. At 7:52 she joined him in the nest and stayed looking through the doorway for nearly a minute, until he pushed past her and flew away. It seemed that she would not begin her morning session until he was present to receive her. This reminded me of a similar display of formalism by a pair of incubating Ringed Kingfishers (*Ceryle torquata*) (Skutch, 1972).

While incubating the woodpeckers from time to time climbed up to look through their doorway. When I tapped on the rotting stub the sitting bird usually looked out, but it was reluctant to leave. The female, which was somewhat more confident than her mate, might even remain in the hole while I set up a ladder and climbed almost to her. When driven from the nest the parent usually clung to a nearby tree and looked on in silence

RUFIOUS-WINGED WOODPECKER

while I inspected the interior with a small mirror and electric bulb. After my return to the ground it soon resumed incubation. To watch the nest we sat in full view a few meters away, apparently ignored by the woodpeckers.

On 25 March one egg was pierced, and by the following morning both had hatched after 12 or 13 days of incubation. The empty shells remained in the nest for at least three days but vanished during the next three days.

NESTLINGS

Development.—The newly hatched woodpeckers had no trace of down on their pink skins. Their eyes were tightly closed, and each had a prominent white egg tooth at the tip of its upper mandible. After a few days I noticed conspicuous white projections or knobs at the corners of their mouths. When they were six days old I could detect, in the mirror that I used to view them in the nest, their feather rudiments as dark spots beneath transparent skin. They now made a buzzing sound. At nine days their pinfeathers, especially the remiges and rectrices, were becoming prominent. The uropygium was conspicuously swollen. The egg tooth was still present. At 13 days the nestlings had long pinfeathers and open eyes. The knobs at the corners of the mouth were less prominent. The egg tooth had vanished from the bill of one but seemed to be present on the other. At 16 days the feathers, especially the largely rufous remiges, were expanding; the knobs at the mouth corners were disappearing; and the egg teeth had vanished from both nestlings.

When it was 19 days old I first saw a nestling climb up to look through the doorway. It stuck its head out, then withdrew, and pecked at the top of the nest chamber. Twice it uttered a high, grating note that lacked the nasal quality of the adults' call. This was the last day that I illuminated the nest to see the young inside, as they were nearing the age when disturbance might cause premature departure. Their expanding feathers now left little skin exposed. The knobs had almost vanished from the corners of their mouths.

Brooding.—On 28 March the two-day-old nestlings were brooded continuously through the first six hours of the day, from 5:30 to 11:30. The male brooded for 103 minutes, the female for 173, then the male for 84 minutes. He was still in the nest when I left at 11:30. During the same hours on 2 April the male brooded for intervals of 32, 45, and 20 minutes, the female once for 90 minutes, making a total of 187 minutes. Thus, the week-old, still naked nestlings were brooded for no more than 52 per cent of the bright, warm morning. On 8 April the 13-day-old nestlings were scarcely brooded. A parent remained with them in the nest for at most four or five minutes at a visit and may have been engaged in other activities, such as feeding and cleaning the nest. By 14 April even nocturnal brooding had ceased.

Feeding.—As in the related Golden-olive Woodpecker (*Piculus rubiginosus*), the nestlings were always fed by regurgitation, the method followed by a

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number of woodpeckers that subsist largely upon ants but not by those that eat larger items, including fruits. Since food was never visible in the bill of a parent approaching the nest, I could not be certain how many times the young Rufous-wings were fed until they were old enough to take their meals at the doorway. It was obvious, however, that the parents brought food much less frequently than do woodpeckers, such as species of *Centurus* and *Melanerpes*, that carry food visibly in their bills. Assuming that every visit to the nest was a feeding visit, each parent Rufous-wing brought food to the two-day-old nestlings only once during the first six hours of the day. Possibly, as when pigeons feed newly hatched young, this food was doled out little by little, in many installments, during the long periods that each parent spent with the nestlings.

To the seven-day-old nestlings, each parent brought food twice in six hours. The meal was now delivered rapidly; the day's first was apparently brought by the female at 6:34, and she was down in the nest no more than two minutes before she emerged with a billful of waste matter. When the nestlings were 13 days old each parent came to the nest thrice, and apparently fed them, in the first six hours of the day. When 19 days old the nestlings were also apparently fed six times, thrice by each parent, in six hours of the morning. Now the parent was often with them for a minute or less, doubtless delivering food.

When the nestlings were 19 days old I first saw a parent feed them without entering the hole. In the middle of the morning the female arrived, clung in front of the doorway, and stuck her head in many times, making movements of her head and neck as though regurgitating, also opening and closing her bill. She continued this for three or four minutes, which was much longer than either parent remained inside feeding them on this morning, then she left without having entered. The nestlings remained invisible during this episode, but soon after this I saw a young woodpecker's head in the doorway for the first time.

Three days later, when the nestlings were 22 days old, I had my first satisfactory view of the act of feeding. At this stage I nearly always found a well-feathered head looking through the doorway. When its father arrived the nestling at the entrance drew back inside and the second young woodpecker appeared in the top of the cavity. The two rested side by side while the parent, clinging in front of the doorway, rapidly poked his bill into their open mouths, alternately, many times. I could not detect any food during this transaction.

Sanitation.—I first saw a parent remove waste from the nest five days after the nestlings hatched. Since the nest had remained clean during these days, probably the parents had swallowed the droppings. On the morning when the nestlings were seven days old the parents removed waste twice in six hours; when they were 13 days thrice in the same interval; and when they were 19 days old once in six hours. As in other woodpeckers that do not use the nest as a family dormitory, including the Golden-fronted (*Melanerpes aurifrons*) and Hairy (*Dendrocopus villosus*), the sanitation of the

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nest was neglected after the parents no longer descended to the bottom to feed their young, who doubtless clung to the side wall even before they took their meals through the doorway.

The parents took equal shares in cleaning the nest. They carried out large billfuls of feces mixed with wood particles. To replenish the supply of this vehicle for removing waste, they loosened fragments from the top of the nest chamber. On 2 April, when the nestlings were a week old, the female interrupted brooding for several minutes while she pecked into the wall at the back of the chamber, as I could see through the doorway. Although most of the loosened fragments dropped into the bottom of the nest, many flew out through the doorway, while others fell upon the doorsill and were left there. Later that same morning the male spent five minutes tearing particles from the top of the wall at the back. He lost fewer than his mate did.

DEPARTURE OF THE YOUNG

While incubating and feeding nestlings the parents foraged where I neither saw nor heard them. Early on 19 April, however, I heard much calling by Rufous-winged Woodpeckers off in the woods. A young bird was looking through the doorway and presently was fed by her mother, then by her father, each time very briefly from the outside. After her second meal she stuck her head out and delivered calls much like the adults'. She was restless, pecking at the wall in the top of the chamber and removing fine fragments of wood, which she dropped, sometimes outside. After a while she clung quietly in the top of the nest. Then she became active again, pecking and sticking her head through the doorway, only to draw it in again. Finally, at 8:37, while the parents were absent, the young woodpecker flew out, alighted competently on a slender trunk 5 m from the doorway, and immediately started to peck at it. She flew to a more distant trunk and called twice. Three minutes after her emergence she flew off through the woods and was lost to view. Her departure left the hole empty.

An hour after this young woodpecker's first flight her father alighted in front of the nest, looked in many times, peered around, and called. He climbed up the nest stub and called again. Soon he returned to inspect the empty nest, more briefly than the first time. The absence of his progeny seemed to perplex him. After more calling he flew off in the direction the fledgling had taken and apparently found her, as I heard much calling in that part of the woods. Finally I spied the young woodpecker on a high branch, from which she appeared to pick and swallow something that did not look edible. Her father darted excitedly among the surrounding trees, twitching his wings rapidly when he alighted. Clinging high on a slender, upright branch, he preened vigorously, revealing the rufous beneath his wings. The fledgling continued to climb restlessly over the treetops, calling frequently, her father occasionally answering. I could not find the other young woodpecker, which had evidently left the nest on the preceding day

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and was off in the forest with her mother. The nestling period of these woodpeckers was approximately 23 and 24 days.

That evening neither a parent nor a juvenile came near the nest, which remained deserted until I pushed it down for examination. While I watched the deserted hole in the dusk, a tayra (*Eira barbara*) came by and sniffed at the base of the stub. Possibly, if the young had not already left, he would have climbed up and torn open the cavity to reach them.

Two weeks after the young birds' departure I watched the father and a daughter foraging in treetops near the nest. The first gave to the second something that he carried inside rather than visibly in his bill. I searched in vain for a second brood. The combined incubation and nestling periods of the Rufous-winged Woodpecker, about 36 days, are about as long as the nestling period alone of the slightly larger Golden-naped Woodpecker (*Melanerpes chrysauen*). The more rapid development of the former is difficult to account for in the light of present knowledge.

The two juveniles raised in the nest that I studied were similar to the adult female, as stated by Ridgway (1914). I have seen no description of the young male. On 1 July 1975 I watched one foraging with an adult male in the trees around our house. Although the young woodpecker appeared to find much food for himself, the adult still fed him by regurgitation, on each occasion seeming to pass rapidly several items or installments of food too small to detect. The juvenile's crown and nape were as bright red as the adult's, but he lacked red on the forehead and malar region. His bill looked slightly shorter than the adult's. Otherwise, he closely resembled his parent.

SUMMARY

An inhabitant of humid lowland forests from Caribbean Honduras to southern Costa Rica and (at least formerly) western Panama, the Rufous-winged Woodpecker usually forages on high, slender branches, pecking shallowly into decaying wood and knot holes.

The high, sharp, nasal calls of this woodpecker have a peculiar twang that makes recognition easy. It beats prolonged, rapid tattoos.

The only known nest was 3.5 m up in a rotting stub in tall, second-growth woods. In early March the two sexes worked by turns, each for intervals of one to three hours, alternately pecking into the soft wood and throwing out chips, once 503 billfuls in 131 minutes. While one partner carved the other was out of sight. When the two met at the nest during construction, they repeatedly seized each other's bills, in symbolic (or perhaps actual) courtship feeding. Nest carving took eight days or a little more. The finished cavity was 40 cm from top to bottom.

The first egg laid in this cavity promptly vanished but, after an interval, two more were laid. These glossy white eggs were incubated by the male through the night and much of the day. On most days the female took one session of six or seven hours, from early morning to early or midafternoon.

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With the exception of one day when this pattern was not followed, the eggs were continuously attended. The two daily changeovers were effected without ceremony.

The incubation period was 12 or 13 days.

Both parents brooded the nestlings, continuously when they were two days old, but only half the morning when they were a week old, and scarcely any when they were 13 days old.

The young were fed by regurgitation, on one visit by each parent during six hours of the morning when they were two days old, two visits when they were seven days old, and three visits by each parent when they were 13 and 19 days old.

Both parents cleaned the nest, carrying out large billfuls of feces mixed with wood chips. To replenish the supply of chips they dug into the top of the nest chamber. After the young took their meals through the doorway, sanitation was neglected.

The young emerged from the hole when 23 or 24 days old and promptly became active, flying well and pecking on trees. After their departure neither they nor a parent returned to sleep in the nest. A parent fed a juvenile two weeks after it left the nest.



FIG. 5. Buff-throated Woodcreeper, *Xiphorhynchus guttatus*.

Family DENDROCOLAPTIDAE
BUFF-THROATED WOODCREEPER

Xiphorhynchus guttatus

One of the larger woodcreepers, the Buff-throated is about 22 cm long. The sexes are alike. Both have the crown and hindneck blackish, thickly spotted with pale buff. The back and wing coverts are olive-brown, rather sparingly streaked with buff bordered narrowly with black. The rump, tail, and remiges are plain cinnamon-rufous. The dusky sides of the head are finely streaked with buff. The chin and throat are buffy to nearly white and unmarked. The more posterior underparts are buffy brown, with pale buffy, black-margined streaks on breast and sides. The eyes are brown. The long, strong bill has a dull black upper mandible and pale grayish lower mandible. The legs and toes are dark gray.

The species ranges from Guatemala to Bolivia, Amazonian Brazil, Rio de Janeiro in coastal Brazil, and Trinidad and Tobago. In Central America it is found throughout the Caribbean lowlands from Darién to the lower Motagua Valley in Guatemala, but on the Pacific side only in Costa Rica and Panama. In Guatemala and Honduras it seems not to occur above 500 m, but in Costa Rica it ranges from the coasts up to about 750 m. In Panama it appears not to have been recorded above 600 m. However, in Venezuela it extends upward to 1,900 m in the Subtropical Zone (Land, 1970; Monroe, 1968; Carriker, 1910; Wetmore, 1972; Phelps and Phelps, 1963).

In the Térraba Valley of southern Costa Rica, where chiefly I have studied it, the Buff-throated Woodcreeper and the Tawny-winged Dendrocincla (*Dendrocincla anabatina*) are the most abundant members of their family in the heavy rain forests, now sadly depleted by agriculture and grazing. From their woodland home both species venture forth into clearings with scattered large trees, where they meet the Streaked-headed Woodcreeper (*Lepidocolaptes souleyetii*), a bird not often seen well within the forest. The Buff-throated Woodcreeper is also common in the tall Caribbean rain forests of Costa Rica, and it even occurs in the heavier woodlands of Guanacaste, the northwestern province where the dry season is long and severe. In Panama Wetmore (1972) considered it to be the most common woodcreeper, found not only in the dense forests of Bocas del Toro and Darién but in trees bordering streams and the landward edge of mangrove swamps in savanna areas. Unsocial birds that seem at most to form transitory pairs, Buff-throated Woodcreepers are usually solitary, although sometimes they accompany mixed flocks of woodland birds. Unlike the Barred Woodcreeper (*Dendrocolaptes certhia*) and several species of dendrocinclas, they only infrequently join the avian crowd that gathers around hunting army ants.

Buff-throated Woodcreepers forage in the manner typical of their family, climbing up trunks to which they cling with strong toes, while they prop

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themselves with the sharp-pointed projecting shafts of their 12 long, stiff tail feathers. Often they start low on a trunk, sometimes at ground level, and work upward in a more or less spiral course until they vanish amid the foliage of the tree's crown. Or they may climb outward along branches, to which they sometimes cling with back downward. They glean insects and spiders from crevices in the bark or the moss and lichens that encrust it. Once I watched one of these woodcreepers ascend a decaying stub upon which grew an aroid whose flat, roundish juvenile leaves were closely appressed to the wood. With its long bill the bird lifted up leaf after leaf to look for creatures hiding beneath them. It also found food on the underside of a rotting bracket fungus.

While I stood watching a mixed flock of small woodland birds, I heard the pleasant notes of a Buff-throated Woodcreeper. Suddenly the brown bird alighted upon a palm trunk within arm's length. Clinging upright to the farther side of the slender trunk, it peered around the side to scrutinize me with bright, dark eyes. After we had gazed intently at each other for a few moments, it flew off to search for insects on neighboring trunks with rougher and more promising bark. A minute later another Buff-throated Woodcreeper (its temporary mate?) flew from a mossy trunk two meters away with a bug in its bill. On another occasion I watched a woodcreeper probe into the grapelike cluster of fruits hanging at the top of the tall, spiny stem of an *Acanthorhiza* palm, and remove a lizard half as long as itself.

FOOD

These woodcreepers appear to eat only animal food, chiefly insects. Haverschmidt (1968) recorded Coleoptera, Arachnoidea, Hemiptera, Homoptera, Hymenoptera (Formicidae), and Orthoptera (Blattidae). Wetmore (1972) found that they had eaten Tenebrionids, Cerambycids, Elaterids, and Cucurionids among beetles, also roach egg cases, cicadas, earwigs, caterpillars, and a small lizard. In addition to a variety of insects, a parent feeding nestlings brought a few spiders and small anolis lizards.

SLEEPING

Like other woodcreepers the Buff-throated sleeps in an old woodpecker's nest or some other cavity in a tree, always alone, as far as I know. Their dormitories are hard to find because the birds retire late, when their dark forms are difficult to distinguish from the dark trunks up which they creep, and they fly out very early in the morning, while the light is dim. To compensate for the difficulty of following them with the eyes, woodcreepers in general are noisy as they seek their dormitories, and where numerous they fill the woodland with their varied calls as the day ends. Once I saw a Buff-throated Woodcreeper slip at nightfall into an old, abandoned hole of one of the larger woodpeckers—the Lineated or the Pale-billed—4.5 m up in a slender, barkless trunk in a bushy clearing near forest. E. O.

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Willis found a Buff-throated Woodcreeper sleeping alone in a cavity only one meter above the ground on Barro Colorado Island (Oniki, 1970).

VOICE

Buff-throated Woodcreepers use their strong voices freely. In the nesting season, chiefly from February or March to June, they make their presence known in humid lowland forests of southern Central America by tireless singing. Clinging to some trunk amid concealing foliage or vine tangles, they repeat clear, far-carrying, melodious notes that at various times I have written *doy doy doy . . .*, or *wic wic wic . . .*, or *weet weet weet . . .*. The song consists of about seven to 16 of these ringing notes, often seven or eight, all very much alike, except that they may be loudest in the middle of the series. This sequence is sometimes followed by several drawled notes of quite different tone: *cheeer cheeer cheeer . . .*, delivered in falling cadence.

This memorable vocal performance may be heard at any hour of the day, but most frequently in early morning and late afternoon, especially if the sun breaks through the clouds after an actual or threatened shower. The woodcreeper's persistent singing, day after day in the same place, coupled with my failure to find a second bird in attendance at two carefully studied nests, leads me to believe that males establish mating stations, to which they may attract one or more females by their voices. I have not found two singing so close together that they could be considered to form a courtship assembly or "lek." In addition to persistent singing while clinging unseen high in trees, the woodcreepers also sing as they forage, climbing up trunks and moving from tree to tree.

In the forest the sexes of woodcreepers can be distinguished only by behavior. One attending a nest and, therefore, most probably a female, was not seen to deliver series of *doy* or *wic* notes. But she did utter the *cheeer*, often loud and clear, and a drier note, *chu* or *choe*, that seemed to express uncertainty or anxiety. Sometimes the *cheeer* was slightly trilled.

NEST AND EGGS

I searched for Buff-throated Woodcreepers' nests for many years before I found one in March 1972. It was situated in the big clump of tall timber bamboos in front of my study window, but on the farther side of the clump, close beside a large tract of rain forest. The nest cavity was in a broken bamboo stem that had long been dead and was blackening with decay. Five and a half meters above the ground a roundish opening, 5 cm wide by about 8 cm high, gave access to the central hollow, which was 10 cm in diameter. The first septum or transverse wall below the doorway was no longer present, perhaps having been removed by the woodcreeper, and the nest rested upon the second one, 50 cm below the doorway. Above this floor the cavity had been filled to a depth of at least 18 cm with hundreds, if not thousands, of pieces of stiff bark, ranging in size from 64 by 50 mm and 85 by 30 mm down to innumerable tiny fragments that had probably

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broken from larger pieces after they had been taken into the cavity. After drying the thickest piece weighed 3.7 grams, the two largest flakes 3.2 grams and 3.0 grams. The top of this filling of bark, where eggs and nestlings had rested, was 30 cm below the doorway.

Since the nest was not opened until it seemed unlikely that it would be used for a second brood, and the bark fragments had decayed and become compacted during many rainy weeks, probably the filling had originally been higher, so that the freshly laid eggs had rested less than 30 cm below the doorway. Above the nest two other transverse partitions were largely intact, although so rotten that they readily fell out when we examined the nest. The nest cavity, however, was not open to the sky through the broken-off end of the hollow bamboo stem.

Until three years later I was uncertain whether the doorway had been made by the woodcreeper, but I doubted that a woodpecker or some other bird had done it. In March 1975 I found a woodcreeper, probably the same individual, preparing a nest in the same bamboo clump where a brood had been raised in 1972. This time the roundish doorway was 6.5 m up in a blackened stem far advanced in decay, on the exposed side of the clump rather than against the forest. Early in the morning of 3 March the woodcreeper brought six pieces of bark or lichen in 25 minutes, always entering headfirst. Later that same morning she came seven times with bark in 17 minutes. Two days later she brought five pieces in 11 minutes. These spells of rather concentrated activity were separated by long intervals when I did not see her near the nest.

While building the woodcreeper was always alone, although once I heard another Buff-throat off in the forest. She never brought more than a single piece of material, held in the end of her strong bill. Sometimes the length of the piece exceeded the width of the doorway. The material could have been inserted end-first, but instead of following this procedure the woodcreeper dropped it when her struggles to pass it through the doorway while held by the middle proved ineffectual. Then she pecked at the rim of the aperture to enlarge it. She hammered like a woodpecker, making taps audible 15 m away, and sometimes detaching visible fragments of the rotting wood. She continued this for some time. At midday on 5 March she came without material, pecked a little at the doorway's edge, then entered, to remain within for 28 minutes, from time to time looking out. Then she emerged and pecked for three minutes, removing small fragments from the rim, after which she reentered and stayed for nine minutes. By 7 March the woodcreeper appeared to be incubating in this nest, but a few days later it was abandoned. These observations left no doubt that if the woodcreeper had not made the doorway to the nest cavity, she at least enlarged it, possibly starting at a smaller hole resulting from decay.

In 1972 I found a late nest in a strangling fig, about 45 m from the bamboo clump where an earlier brood had been successfully raised. The entrance to this nest was 2.2 m up in the network of thick, anastomosing roots that the fig had thrown around a muñeco tree (*Cordia bicolor*) in

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a pasture, close by the forest. The doorway was 33 cm high but only 2.5 cm where widest; I could not insert my hand, laid flat. The bird had evidently not tried to enlarge this opening in living, latex-rich bark and wood that would doubtless have resisted her bill. The eggs lay only 5 cm below the lower end of the aperture, on a bed of large flakes of bark, where they were plainly visible from in front without using artificial illumination or a mirror. The space between the roots where they rested was about 30 cm high, 15 cm from front to back, and even wider from side to side. It was very much roomier than the hollow in the bamboo.

Buff-throated Woodcreepers use a variety of nest sites. On 14 April 1937 Chapman (1938) found a nest beneath the elevated floor of a building set on posts in the narrow clearing amid the forest on Barro Colorado Island. The woodcreeper had deposited here more than 7,000 fragments of bark and dead wood. In Trinidad two eggs of this species were found in a hole in a dead stump, 2.5 m up, resting on a bed of weed stems, dead leaves, and plant down (Belcher and Smooker, 1936). This material might have been carried in by some other bird before the woodcreeper acquired the cavity.

In the first nest in the bamboo incubation began about 18 March. It was impossible to see the eggs in this nest without risking the collapse of the decaying stem that held them. The nest in the fig tree contained, on 15 July 1972, two eggs that could be removed intact with a long spoon. They were pure white, glossy, slightly tapering, and almost equally blunt at the two ends. They measured 30.0 by 19.9 and 27.0 by 19.0 mm. In Trinidad and Tobago five nests of the race *X. guttatus sussurans* have been found in March, June, and July (French, 1973). There, also, the set consists of two white eggs, of which four averaged 30.0 by 22.4 mm (Belcher and Smooker, 1936). Haverschmidt (1968) gave the measurements of eggs from Surinam as 26.5 by 20.1 mm.

INCUBATION

We spent a total of 28 hours watching the two nests during incubation, including one all-morning watch at each and an all-day watch at the nest in the bamboo. At no time were two woodcreepers in view, or one in sight while one was in the nest; although rarely a second woodcreeper called in the neighboring woods and was answered by the attendant bird. The latter sat for long intervals, separated by long absences. Eight sessions timed in full at the two nests ranged from 91 to 181 minutes and averaged 121.6 minutes. Nine recesses varied from 25 to 47 minutes and averaged 33.1 minutes. On 24 March the woodcreeper first left her nest in the bamboo at 6:17, nearly an hour after early dawn, and she returned, to stay until nightfall, at 15:21, nearly three hours before dusk. During her active period of nine hours and four minutes, she took only three sessions and four recesses and was in her nest 80 per cent of the time.

When returning to the nest for another spell of incubation the woodcreeper

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often carried in material, sometimes apparently several pieces at one time. Far from silent, she sometimes called loudly with *cheeer* or *chu* notes while approaching the nest, just after leaving, with her head in the doorway, or even while down inside hidden from view. After leaving her nest in the bamboo early one afternoon the woodcreeper continued for nearly a quarter of an hour to call *chu*, and less often *cheeer*, while clinging to neighboring trunks, now high, now low. Once I heard an answering *cheeer*. Small army ants (*Labidus*) were at this time swarming near the bamboo clump, with a variety of attendant birds, including a Tawny-winged Dendrocincla. Whenever I stood in front of the low nest in the fig tree and made a slight noise, the incubating woodcreeper emerged and climbed unhurriedly up the trunk, as though not much alarmed.

At the bamboo nest incubation apparently began on 18 March, the first day I found the woodcreeper in the nest in the afternoon. On 4 April she was still carrying bark into the nest but by the following day she was taking in small insects, indicating that at least one egg had hatched. The incubation period was about 18 days, one day longer than that determined at the nest of a Spot-crowned Woodcreeper (*Lepidocolaptes affinis*) into which I could look.

At the late nest in the fig tree incubation continued from at least 15 July, when I found the nest already with two eggs, until 13 August, after which I no longer found the bird in attendance. Opening the eggs after their abandonment I detected no trace of an embryo.

NESTLINGS

In 22 hours of watching while young were in the bamboo nest I had no indication that two parents were attending them. Not only did I consistently fail to see two bring food at about the same time, but while one was brooding for long intervals no other ever came near the nest. Therefore, I concluded that the female parent raised the nestlings alone, as she had built and incubated alone.

After the nestlings hatched the parent sometimes darted so rapidly from her doorway, surrounded by stout bamboo stems, that I missed some of her departures and could not time all her periods of brooding. During the morning of 7 April, when the nestlings were about two days old, they were brooded for 45 and 49 minutes and for two other intervals of undetermined length. During the forenoon of 12 April the week-old nestlings were apparently brooded for one interval of 13 minutes when the parent remained down in the nest, but on no other visit with food did she stay more than a minute or two. Thereafter I recorded no more daytime brooding. Even nocturnal brooding ceased when the nestlings were nine or 10 days old.

In the first six hours of 7 April the two-day-old nestlings were fed seven times. In the corresponding period of 12 April the week-old nestlings were fed 13 times and in the first six hours of 21 April the 16-day-old nestlings

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received food 12 times. If, as I believe, two nestlings were present, this was one item per nestling per hour. From 5:15 to 6:00 on 23 April the parent brought food three times and from 5:15 to 6:05 on the following day she also fed three times. Now, when the nestlings were 19 days old I for the first time saw the parent pass food through the doorway, without herself entering the cavity.

In contrast to the habit of many Oscines, which may bring several items of food in their bills or mouths at one time, but in common with members of such related families as antbirds and ovenbirds, the parent woodcreeper always brought a single item, held conspicuously in the tip of her bill. Nearly always the item was an insect which, after the nestlings' first week, was often quite big. Twice I saw the parent take a large spider to the nest, and three times a small *Anolis* lizard, with its colorful gular sac conspicuously protruding.

At least some of the droppings were carried away in the parent's bill. When the nestlings were 16 days old she removed seven of these conspicuous white objects in six hours.

More cautious now than while she incubated, the parent never called while at the nest, and rarely just after flying from it. After entering the nest with food she nearly always turned around to look out briefly before descending into the hollow to deliver what she had to the nestlings. As to the young woodcreepers themselves, I neither saw nor heard them while they remained in their nest. Their silence contrasted greatly with the loquacity of nestling Streaked-headed and Spot-crowned woodcreepers that call much at mealtime or while waiting for their food.

Early on 24 April the parent was still taking food into the nest. At 5:32 on 25 April she arrived with a large mangled insect in her bill and clung in front of the doorway, while I heard long-continued calls that seemed to emanate from the midst of the bamboo clump behind the nest. After hesitating at the doorway for several minutes, the parent called *chu chu*, then flew toward the river. Soon she returned to the doorway with the same insect, only to carry it away the second time. Once more she alighted in front of the doorway, from which she flew into the midst of the bamboo clump with her insect. There, apparently, she found and fed a fledgling that had left the nest since the preceding morning, aged about 20 days. This is nearly the same as the 19-day nestling period of the Streaked-headed and Spot-crowned woodcreepers, but substantially shorter than the 24-day period of the Tawny-winged Dendrocincla.

Sounds that I heard issuing from the thick, densely crowded bamboo stems suggested the presence of two fledglings; although I peered into the clump for hours without glimpsing more than one at a time, and that but fleetingly as it flew from one stem to another. Until the sun was high I heard a confusing amount of calling from one or more woodcreepers among the surrounding trees, answered in weaker tones from the young hiding in the bamboo clump. The fledglings seemed already able to utter most of the adults' notes, but with less volume. As well as I could see

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from very brief glimpses, they closely resembled their parent.

Late in the morning the young woodcreepers left the bamboo clump. Neither they nor their parent returned to sleep in the nest cavity, which remained deserted after their departure.

CONCLUSIONS

It is becoming increasingly clear that two contrasting mating systems occur in the woodcreeper family. In the genus *Lepidocolaptes*, as exemplified by the Streaked-headed and Spot-crowned woodcreepers, enduring pairs are formed and both sexes build, incubate, brood, and feed the young. The same pattern of parental cooperation is found in the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) (Skutch, 1969). In the genus *Dendrocincla*, exemplified by the Tawny-winged Dendrocincla (*D. anabatina*) (Skutch, 1969) and the Plain-brown Dendrocincla (*D. fuliginosa*) (Willis, 1972), males take no share in incubating or attending the young. Incomplete observations suggest that this is also true of the Olivaceous Woodcreeper (*Sittasomus griseicapillus*) (Skutch, 1967). To these species of which males remain aloof from the nest we may now add the Buff-throated Woodcreeper. Many additional studies are needed to reveal the distribution of these two patterns of parental care among the 60 species of the Dendrocolaptidae.

Is it only a coincidence that nestlings of *Lepidocolaptes*, attended by both parents, are loquacious, whereas those of *Dendrocincla* and *Xiphorhynchus*, attended by only one, are silent?

SUMMARY

A solitary inhabitant of lowland rain forests, the Buff-throated Woodcreeper hunts in the manner typical of its family, climbing up trunks and outward along branches, gleaning insects and spiders from crevices in bark or incrustations of mosses and lichens. It varies its diet with an occasional small lizard.

These woodcreepers sleep singly in old woodpeckers' holes or other cavities in trees, retiring late and emerging early, while light is dim.

Clinging amid concealing foliage or vine tangles, they tirelessly repeat a loud, clear, ringing note, chiefly in the breeding season from February or March to June. This utterance apparently advertises the mating station of a solitary male, that will form no lasting nuptial bond. These noisy woodcreepers have a variety of other calls.

The nest is built in a cavity, which may be a hole in a trunk, the hollow interior of a timber bamboo, between the roots of a strangling fig, or a nook in a building close by forest. If the entrance is narrow the woodcreeper may enlarge it by woodpeckerlike pecking. She carries in many flakes of bark, often forming a deep accumulation, on which she lays two white eggs.

The female alone incubates unattended by a mate. Her sessions, which often last from 1.5 to 3 hours, are separated by recesses that last about

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half an hour. One female, watched for a full day, was in the nest 80 per cent of her active period. Returning from an outing she often brought a piece of bark to add to her already great accumulation. She was far from silent.

At one nest the incubation period was about 18 days. A female incubated infertile eggs for at least 29 days.

At one nest only a single parent attended the young. The rate of feeding ranged from seven times in six hours when the nestlings were two days old to 13 times in six hours when they were older. On each visit she brought a single insect, spider, or lizard, held conspicuously in the tip of her bill. She carried out droppings.

In contrast to the loquacious nestlings of *Lepidocolaptes* spp., these nestlings were not heard until they left the nest, aged about 20 days. Neither they nor their parent returned to sleep in the nest space.

The Dendrocolaptidae exhibit two contrasting breeding patterns. In *Lepidocolaptes* and *Glyphorhynchus* both parents incubate, brood, and feed the nestlings. In *Dendrocincla*, *Xiphorhynchus*, and apparently *Sittasomus*, males remain aloof from nests.

WEDGE-BILLED WOODCREEPER

Glyphorhynchus spirurus

When I wrote my earlier account (1969) of this smallest of the woodcreepers, I had found it sleeping, always singly, in a cavity resulting from decay in a low stub in eastern Ecuador, and in a crevice between the buttresses of a decaying stump in the Caribbean lowlands of Costa Rica. The higher of the two nest cavities that I had seen was only 80 cm above the ground, in a rotting stump. None of the few that I had found recorded in the literature was much higher; one was so low that the eggs rested at, or below, ground level, although the doorway was 25 cm up. I had not at that time seen the record (Russell, 1964) of a nest 2.5 m up in a shallow cavity in the base of a dead palm leaf in British Honduras (now Belize), which held two eggs on the surprisingly late date of 5 October. I had watched a pair of Wedge-bills incubate through a morning, sitting alternately and keeping their two plain white eggs constantly covered, but I lacked observations on the care of nestlings.

A HIGH NEST

As I walked through the forest at Los Cusingos on the morning of 8 April 1969, the calls of a Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) drew my attention to a thick, irregularly ridged and furrowed trunk. For many minutes the big woodcreeper clung to this trunk and to neighboring palm trees, repeating over and over a full, slurred note, and often going to peer into a furrow that led down into a closed space. Sometimes the

WEDGE-BILLED WOODCREEPER

bird entered this furrow, although I did not see it descend into the enclosed part. Clinging beside the opening it pecked nervously at the bark and twitched its wings. It appeared to be seeking a nest chamber but afraid to enter the dark cavity. Once a Wedge-bill flew toward the much bigger woodcreeper.

Continued watching revealed that a pair of Wedge-bills were incubating in the hollow that interested the Buff-throated Woodcreeper. Possibly the presence of one of the former, and the threats that it made, prevented the big woodcreeper from entering. The lowest part of the opening that led into the closed space was about 6 m above the ground, by far the highest entrance to any Wedge-bill's nest known to me. We did not succeed in learning how far below the opening the eggs rested; it could have been many centimeters because the ridges, some of which had grown together enclosing the intervening furrows, ran a long way up and down the trunk. When the nest was discovered the parents were taking turns incubating eggs that were near the point of hatching, as three days later they were carrying in food for nestlings.

NESTLINGS

The discovery of this nest gave an opportunity to answer a question of long standing: How do Wedge-bills feed their young? Since I had so often watched them climbing up trunks, incessantly pecking at the bark and apparently eating creatures too minute for me to detect from the ground, I surmised that they might feed by regurgitation, like other birds that nourish their young with many small items, such as ants or grass seeds. However, as far as I knew, all the larger woodcreepers bring insects held visibly in their bills, one at a time.

I watched this nest throughout the morning of 11 April. The nestlings had hatched and the parents were bringing them very small items, sometimes barely visible in their bills, at other times apparently completely enclosed in them. Rarely I recognized a tiny insect. I could not learn the number of nestlings nor how many times they were fed. If they received food each time a parent entered the nest, the number of feedings was 12. From 5:15 to 11:05, 12 periods of brooding ranged from 2 to 44 minutes and totaled 266 minutes. The nest was unattended for seven intervals, ranging from 1 to 20 minutes and totaling 84 minutes. The nestlings were brooded for 76 per cent of the morning. That both parents did so was clear from the five changeovers that I witnessed.

The Buff-throated Woodcreeper continued to be interested in the nest cavity. On 9 April while we tried to reach the nest with a ladder that proved to be too short, it approached with something in its bill but, seeing us, it flew away. While I watched on 11 April the woodcreeper climbed up the trunk of the nest tree, paused in front of the nest and voiced a slurred note. It climbed higher, then descended to the opening and called several times. Without entering it flew away.

I watched this nest again from 5:20 to 10:20 on 18 April. The nestlings

WEDGE-BILLED WOODCREEPER

were fed 20 times by both parents. As far as I could see they were given only insects, brought one at a time. Most were about as large as the parents' bills. Because they were held in the whole bill rather than in the tip, they were difficult to see; but the largest projected slightly at the sides, and sometimes antennae or legs stuck out well beyond the bill. The only one that I identified was a small moth. Early in the morning the nestlings made a sharp, rapid peeping, clearly audible 30 m away, when a parent entered with food. Later, when they had been well fed, I only exceptionally heard their voices at mealtime. The parents usually came and left in silence; rarely one uttered a slight, sharp note. Twice they carried away droppings in their bills.

On the morning of 20 April the Wedge-bills were still feeding their nestlings. When I approached on the following morning the head of a large snake projected from the opening. Probably it had already swallowed the nestlings. Neither by hammering on the trunk nor by throwing sticks could I dislodge it. Soon afterward the nest trunk fell, and I have found no other Wedge-bills' nest.

SUMMARY

Although most recorded nests of Wedge-billed Woodcreepers were low, an exceptionally high nest, 6 m up in a deeply furrowed trunk, offered an opportunity for further study. A Buff-throated Woodcreeper's persistent interest led to its discovery.

Both parents incubated, brooded, and fed the nestlings, bringing small insects held visibly in the bill, one at a time. When about a week old the nestlings were fed 20 times in five hours.

The nestlings were devoured by a snake.



FIG. 6. Streaked-chested Antpitta, *Grallaria perspicillata*.

Family FORMICARIIDAE

RUSSET ANTSHRIKE

Thamnistes anabatinus

In contrast to other antshrikes in which the sexes often differ strikingly, the male and female of the Russet Antshrike are too similar in their plain brown and cinnamon-rufous plumage to be readily distinguished. From southern Mexico to Bolivia, and from the lowlands up to 1,200 m or a little more in Costa Rica and the Andean foothills of southwestern Venezuela (de Schauensee and Phelps, 1978), these 15 cm birds inhabit humid forests. Living in pairs throughout the year, they search for insects amid foliage in the middle and upper levels of the forest—consistently higher than any other antbird that I know. Occasionally they descend to lower levels, and very rarely to the ground. Although I have never seen Russet Antshrikes in flocks of their own kind, pairs regularly accompany the mixed parties of small insectivorous birds that roam through the woodlands. Once I watched one member of a pair, probably the male, feed his mate.

NESTING

In the third volume of *Life Histories of Central American Birds* (1969), I could report only a single nest of this antshrike, apparently the only one ever found by an ornithologist. Situated about 15 m up in a tree just inside the forest's edge, beside a pasture, it was built by both sexes in April 1965, and eggs were laid in it about the beginning of May. Although the nest was inaccessible, I learned that both sexes incubated, brooded, and fed the nestlings. The latter were apparently taken by a predator that left the nest hanging precariously. I watched it fall into a vine tangle where I could not find it.

In the years following the loss of this nest, a pair of Russet Antshrikes, possibly its builders, often foraged, vireo-like, in the shade and fruit trees of our garden and the adjoining pasture, always within a short flight of the high forest. Often while sitting in my study I heard their soft, rather plaintive *cheep cheep cheep cheep* and lower conversational notes that evidently kept the mates in contact.

Soon after 11:00 on 6 June 1974 a hard shower fell. Before noon it stopped and sunshine broke through the clouds. At this time I noticed a pair of antshrikes starting a nest in the spreading mango tree beside the cabin where I write. The site was 7 m up, at the tip of a branch amid clustering foliage that concealed it well, and almost above the edge of the roof. I had often seen the antshrikes foraging together in this mango tree, mostly on wet afternoons. When first noticed both sexes were building actively. From 12:08 to 12:30 I counted 24 visits to the nest by the two of them. As at the earlier nest, each placed its own contribution; as one arrived

RUSSET ANTSHRIKE

with material the other, if sitting in the nest site, promptly left. Much of the material was gathered in the mango tree itself. The only note that I heard from the building birds was a low, reiterated *weet*. At 12:30 the pair flew away. In the late afternoon they resumed work and continued until about 17:00. On the following day I did not notice the antshrikes in the mango tree, but on the morning of 8 June they built a little more, bringing pieces of dead leaves.

This nest was so situated that I could not reach it either with a ladder or by climbing the tree. However, by climbing the mango tree and using a mirror attached to a long, thin pole, I could with difficulty glimpse the nest's contents through obstructing foliage. The first egg was laid on 12 June. Early the following afternoon I found an antshrike sitting in the nest for the first time. The second and last egg appeared on the morning of 14 June. Two days later only fragments of shell remained in the nest. Apparently some small mammal, probably a squirrel (*Sciurus granatensis*), had plundered it.

We cut down the empty nest for examination. The deep, vireo-like pouch was attached by its rim to the two slender, leafy arms of a fork. Its walls curved inward so that it was wider near the bottom than at the top, a configuration that made it less likely that the wind could shake out the eggs. It was composed largely of a thick layer of dead leaves, held together by fine, dark strands that appeared to be in part rootlets and in part fungal rhizomorphs. These filaments looped over the supporting twigs, surrounded the body of the nest in a very open network, and were intercalated with the leaves. The outermost leaves were largely of dicotyledons, some from the mango tree, and were up to 13 cm long by 5 cm broad. The inner layer was composed of thinner, narrower leaves from a neighboring timber bamboo. Above this a few dark strands completed the lining. A spray of creeping polypody fern with a threadlike stem and tiny roundish leaves was attached to the outer side, away from the fork. The general aspect of the nest was that of an untidy accumulation of dead leaves, well screened by the living foliage that clustered around it. It measured about 10 cm in height and diameter. The interior was 5 cm wide and deep.

Viewed in a mirror at a distance of several yards, the eggs appeared pale gray with darker marks, especially on the thick end. The fragments of shell that remained in the nest were dull white, finely speckled with brown.

After the loss of this nest the antshrikes no longer visited the garden, and I rarely saw or heard them in the neighboring forest.

SUMMARY

In pairs throughout the year, Russet Antshrikes search for insects in middle and upper levels of humid forest, often in company with other insectivorous birds. Occasionally they forage in scattered trees in clearings, or descend to the ground. The male feeds his mate.

STREAKED-CHESTED ANTPITTA

The first accessible nest, built by both sexes in a mango tree in a garden adjoining rain forest, is described. Two dull white eggs, finely speckled with brown, were laid on alternate days, and soon destroyed by a predator. At an earlier, inaccessible nest, both sexes built, incubated, brooded, and fed nestlings.

STREAKED-CHESTED ANTPITTA

Grallaria perspicillata

In an earlier account (1969) of this plump, almost tailless, long-legged antbird, I told how it hops with feet together over the forest floor, nearly always alone, tossing aside fallen leaves to uncover the small creatures that lurk beneath them. Rarely, especially if alarmed, it flies up to a low perch, usually no more than a meter or two above the ground. An unforgettable song of the Costa Rican forests consisting of about seven to nine mellow whistles in a most peculiar, melancholy tone, puzzled me greatly until I watched an antpitta repeat it over and over while incubating. The two eggs were abandoned unhatched, but not before I had learned that both parents warm them by turns, sometimes sitting as much as five hours continuously. Two nests that I later found also fared badly, with the result that I lacked observations on the nestlings and their care.

Since the publication of my earlier account I have found two more nests of the antpitta, both in the Valley of El General where the first three nests were situated, at an altitude of about 750 m. One of these later nests was amid the rather open undergrowth of secondary woods, dominated by tall trees of *Goethalsia meiantha* that adjoined a large tract of ancient rain forest. The space between two slender saplings was bridged by coarse, decaying twigs, up to 28 cm long, that had evidently been there for some time, as they were stuck together by fungi. On the slight platform made by these sticks, at a height of one meter, was a thin bed of dead leaves, the largest 13 by 8 cm, which had been molded into a depression that the birds had lined with a few fine petioles and tendrils. The overall diameter of the nest was about 20 cm. The concavity was 8.2 cm in diameter by 3.5 cm deep. No sticks supported the center of the nest; when the leaves that formed the cup were removed a large hole remained in the center of the ring of sticks. A few days after I found this nest the two eggs vanished.

Five years passed before I found another antpittas' nest. This was situated beside a little-used path that ran between the old forest and the second-growth woods where the preceding nest had been located. This latest nest was 1 m up in the center of a leafy crown of a small tree fern. The shallow saucer was loosely constructed of short, coarse, dead twigs and small dead leaves that formed a continuous inner layer, above which was a very sparse lining consisting of a few fine petioles and rootlets. Not including the projecting ends of twigs, this nest was about 15 cm in diameter, with a

STREAKED-CHESTED ANTPITTA

concavity 9 to 10 cm inches in diameter by about 2.5 cm deep. Like other antpittas' nests that I have seen, this was precariously situated and carelessly constructed. If I had not propped it up with a forked stick, it would have fallen before the eggs hatched.

The five nests of the Streaked-chested Antpitta ranged from 64 to 150 cm above the ground, with an average height of 1 m. All were beneath tall forest trees.

Each of these nests contained two broad, blunt eggs. On a ground that ranged from pale bluish gray to brownish gray, they were heavily and coarsely mottled with dark brown that on some was almost sooty. The large blotches formed a wreath around the egg's thicker end, or covered it almost solidly. The deep brown pigment covered more than half of the entire surface of some eggs. The measurements of nine eggs average 26.1 by 20.7 mm. Those showing the four extremes measured 28.2 by 21.0, 24.2 by 20.1, and 27.0 by 21.4 mm.

In five nests in the Valley of El General, at about 750 m above sea level, eggs were laid as follows: April, 1; May, 1; June, 2; August, 1.

INCUBATION

The nest found in a small tree fern on 9 June 1975, when it held two newly laid eggs, was exceptionally favorable for study. The antpittas were not shy and sometimes continued to sit while I walked along the path beside which the nest was situated. They were more likely to remain sitting if I refrained from looking at them as I passed at a distance of about two meters. Although at first I watched from a blind, I soon discovered that concealment was unnecessary. The pair of antpittas was not disturbed when I sat in the pathway about 8 m away, watching through a binocular. In addition to long vigils, I made frequent checks on the nest from the path without alarming the birds. Most fortunate of all, a small white patch, evidently a few albinistic feathers, on the mantle of one member of the pair enabled me to distinguish the otherwise quite similar mates. Since the normal partner incubated by night, and in all antbirds of which I could distinguish the sexes I have found this to be the female's task, I concluded that the abnormally marked bird was the male.

The incubating antpittas followed a simple schedule that involved only three long diurnal sessions, two by the male separated by one by the female. On 18 June, when I made an all-day record, the female must have left in the dim light of dawn as the eggs were already cool when I arrived at 5:50. Sixteen minutes later the male arrived, to sit continuously for 6 hours and 4 minutes, or until 12:10 when his mate replaced him. She incubated for 2 hours and 43 minutes, or until 14:53 when the male returned to begin a session that lasted 2 hours and 24 minutes. He left spontaneously at 17:17 and 3 minutes later the female returned to remain through the night.

STREAKED-CHESTED ANTPITTA

Although all my observations fitted into this pattern, the times of arrival and departure of the two partners varied from day to day. Usually the female left the nest at early dawn, but on 14 June she remained on the eggs until her mate came to replace her at 6:46. The interval between her first morning departure and the male's arrival varied from 0 to 47 + minutes. Four of his morning sessions lasted, respectively, for 5 hours and 10 minutes, 6 hours and 29 minutes, 6 hours and 4 minutes, and 6 hours and 13 minutes. (At the first antpittas' nest I timed a morning session, doubtless by the male, only 2 minutes short of 5 hours.) The male ended his long spell of incubation at times ranging from 10:55 to 13:15. Replacing him immediately, or after a few minutes, the female then incubated for two or three hours. The male's afternoon session, much shorter than his morning session, also lasted for two or three hours. One day the female began her night session at 16:18, and on another as late at 17:20. By far the greater part of the daytime incubation was by the male.

Less extended observation at a Great Antshrike's (*Taraba major*) nest suggested a similar pattern of incubation, with the male taking each day two sessions separated by one of the female. At this nest the female took longer diurnal sessions than the female antpitta did. The incubation schedule of the Resplendent Quetzal (*Pharomachrus mocinno*) is similar.

On the few occasions when I saw an antpitta approaching the nest for its turn of incubation, it came hopping over the ground, sometimes tossing aside fallen leaves as it advanced. More often I did not notice the bird until it flew up to the nest. If the mate were still present it promptly left; the changeover was always effected silently, without ceremony. The antpittas also incubated in silence, except that one morning the male stretched up his neck and, his white throat prominent, repeated the *cow cow cow* song in a subdued voice at short intervals for nine minutes, while faint answers came from a distance. One morning, before leaving the nest in the early light, the female sang softly *cow cow cow cow cow*, repeating this thrice. On the morning when her first egg was pipped she remained sitting longer than usual and called twice in a subdued voice.

These antpittas sat motionless for long intervals, only rarely rotating to face in another direction. Resting with neck retracted, they appeared very rotund. The boldly streaked upper breast was visible above the nest's low rim. The light ring surrounding each big, dark eye made the bird appear alert. At intervals it closed its eyes halfway or a little more, never fully, and only for a second or two. Once the male rose in the nest to scratch his head over a wing. The incubating antpitta did not alter its posture when Gray-chested Doves (*Leptotila cassinii*) and a Ruddy Quail-Dove (*Geotrygon montana*) walked over the ground a meter beneath it, nor when an Agouti (*Dasyprocta punctata*) buried a dark, round object, apparently a seed, in the path close beside it. But when a Blue-diademed Motmot (*Momotus momota*) alighted on a branch about 6 m away, the male antpitta sat slightly higher in his nest, with his head tilted upward at an angle of about 30 degrees, and held this pose for the several minutes that the motmot remained

STREAKED-CHESTED ANTPITTA

in view. As soon as the larger bird departed the antpitta resumed his usual posture.

When the female left the nest at 5:09 on 23 June, one egg was pipped. Twenty-five hours later the shell was not pierced. When the female left the nest at 5:45 on 25 June, the egg had hatched and the empty shell had vanished. The other egg failed to hatch. The incubation period was at least 15 or 16 days.

NESTLING

The newly hatched antipitta was blackish on all upper parts, including its stubby wings. Its ventral surface was orange-flesh color. It bore no vestige of down, but feather rudiments were already visible through the skin of its body and wings. Its eyes were tightly closed. The interior of its mouth was bright orange, the bill and oral flanges paler orange, with the tip of the upper mandible blackish. It bore a tiny egg tooth. The nestling's feet were pale, its claws almost colorless. Already it rested upright on its swollen abdomen, its head tucked beneath itself, except when lifted high to gape. It uttered a weak *peep peep peep*. A day later its remiges projected about 1 mm from its wings. When two days old it vanished, along with the unhatched egg, probably the victim of a snake. Thirty-nine years after I found my first antpittas' nest, I have still not seen an older nestling. At least four of the five nests failed; in the fifth, which I could not follow to the end, a single nestling might have been raised.

With the hatching of the nestling the parents' rhythm of sitting changed abruptly. Now, instead of remaining in the nest for long intervals, they came and went frequently. From the female's first morning departure at 5:45 until 11:20 on 25 June, the male brooded the newly hatched nestling for 10 intervals, ranging from 1 to 71 minutes and totaling 232 minutes. The female brooded nine times, for intervals ranging from 2 to 36 minutes and totaling 96 minutes. The nestling was left unattended only twice, for 6 and 1 minutes.

As 25 June dawned the female, which had brooded through the night, rose in the nest, poked down into it half a dozen times, then resumed sitting. When at 5:45 she left the hatchling gaped persistently. Returning at 6:04 she gave it its first meal. Thrice the male arrived without food and settled on the nest without appearing to notice the nestling gaping in front of him. But during his third session of brooding, which lasted 45 minutes, he at intervals rose to poke down into the nest, as his mate had earlier done. This seemed to arouse him to the nestling's need, for when he next returned, at 6:58, he brought food for the first time. By 11:20 the female had fed the nestling nine times, the male, six times. As far as I saw, each meal consisted of a single small insect.

While the male antpitta brooded late in the morning, a great horde of army ants (*Eciton burchelli*) flowed down the slope near the nest and over the path below it. When some of the ants climbed the tree fern to the

STREAKED-CHESTED ANTPITTA

nest, the antpitta picked them off and ate them, perhaps half a dozen in all. Two or three Tawny-winged Dendrocinclas (*Dendrocincla anabatina*) following the ants clung to trunks around the nest, sometimes within two meters of it; but the parent antpitta ignored them, and they him. Soon the deployed swarm of ants moved away, without molesting the nest any more, but until after midday the army's supply column continued to pass over the ground nearby. This was not the first time that I saw army ants, which specialize on invertebrate prey, reach the nest of a small bird without harming it (Skutch, 1977). Although the nestling and unhatched egg vanished from the antpittas' nest two days later, their total disappearance pointed to a predator larger than ants.

SUMMARY

Five nests of the Streaked-chested Antpitta were flimsy constructions of coarse sticks and dead leaves, sparingly lined with fine petioles and rootlets. They were situated from 64 to 150 cm up, beneath tall forest trees. Each contained two broad, blunt, heavily pigmented eggs.

Incubation was studied at a nest where the sexes could be distinguished by an abnormal spot of white on the male's back. The female incubated through the night and left early in the morning. Each day the male took two long sessions, separated by one session of the female. His morning session lasted from 5 to 6.5 hours. Each parent sat for two to three hours in the afternoon. The incubation period was at least 15 or 16 days.

The nestling hatched with no vestige of down. The interior of its mouth was bright orange. In 5.5 hours the newly hatched nestling was brooded 10 times by the male and 9 times by the female parent. He fed it 6 times and she 9 times, each time with a single small insect.

A swarm of army ants flowed by the nest without harming it. The few ants that climbed to the nest were eaten by the brooding male. The ants apparently were not responsible for the disappearance of the nestling and unhatched egg two days later.

Family PIPRIDAE
THRUSH-LIKE MANAKIN

Schiffornis turdinus

My earlier account of the Thrush-like Manakin (Skutch, 1969) told how this plain brown bird lives obscurely in the undergrowth of humid forests, usually within a meter or two of the ground, repeating at intervals a beautiful, tripartite whistle, so ventriloquial that it fails to guide a listener to its source. A solitary bird, this manakin appears never to perform in courtship assemblies or leks, like other species of Pipridae. Without alighting it plucks berries and insects from twigs or foliage, in typical manakin fashion. I described four nests, bulky open cups composed chiefly of whole large leaves or leaf skeletons, and situated in a spiny palm or tangle of vines, 1 to 1.3 m above the ground in the forest. Three of these nests contained each two eggs; the fourth a single infertile egg. They were incubated only by the female, which took very long sessions separated by long absences. One bird, watched from dawn to dusk, covered her eggs 68.8 per cent of the day. At this nest the incubation period was between 20 and 21 days. At no nest was a second bird seen to take an interest. I reported only scanty observations on the care and development of the young, none of which survived for the full nestling period. The present chapter compensates for this deficiency with observations of parental care and nestling development at the first successful nest, the fifth that I have seen.

One afternoon in May when I had set my camera on a tripod to photograph a low, hollow stump in which a pair of Bicolored Antbirds (*Gymnopithys leucaspis*) was attending eggs, a Thrush-like Manakin flew up unannounced. He clung to a slender, upright sapling near the ground and hardly 2 m from me, leaned forward, and, turning his big head slowly from side to side, scrutinized me and my apparatus with large, dark eyes. Then he flitted to a neighboring slender, upright stem to which he also clung only 30 cm or so above the ground, and eyed the strange apparition from another angle. After several seconds here he flew to a third stem and repeated the process. Then he reversed his direction, returned to the first sapling, and behaved as before. All his movements were slow and deliberate. He seemed curious and quite unafraid. Having, I hoped, satisfied his inquiring spirit, he flew off through the underwood, uttered his calm whistle just once, and vanished. I found no manakin's nest nearby.

NEST AND EGGS

The fifth nest was situated a meter up, between the fronds and slender stems of a clump of small *Bactris* palms armed with long, black spines, in old second-growth woods dominated by tall trees of *Goethalsia meiantha* that were dying of old age. The very bulky open cup was composed of

THRUSH-LIKE MANAKIN

a great mass of dead leaves, most of which were 15 to 20 cm long by 5 to 8 cm broad. Many had been reduced by decay to lacy skeletons, a process that continued during the rainy weeks while the nest was occupied. The nest had no proper foundation, the leaves being held in place by the spiny stems and petioles of the palms. The lining consisted of a few blackish fibrous rootlets. The builder appeared to have broken off a few of the needle-sharp thorns on the side at which she habitually entered and left the nest, but so many remained that I marveled that she avoided injury by them. I probably would not have noticed this nest if the parent had not flown out as I walked along the path beside which it was situated, as many similar palm clumps in this woodland had accumulations of fallen leaves at about the same height.

This nest held two glossy eggs, which were pale buff, with a few large and small black and blackish spots on the thicker end. Both measured 24.6 by 19.1 mm. They were laid in early August 1977. The five sets of eggs that I have seen in the Valley of El General show that laying extends from late February to early August, but three of the five were laid in May. In the Mexican state of Chiapas, Alvarez del Toro (1952) found a nest with two eggs, measuring 25 by 19.5 mm. on 5 August 1949. This nest, much like those that I have seen in Costa Rica, was among palm fronds 50 cm above the ground. In Belize, on 1 March, Edwin Willis discovered a nest 60 cm above the ground in the stump of a palm. It was composed of leaf skeletons and lined with a thin layer of fine rootlets, on which rested two eggs. Five weeks later one young had left this nest, which was afterward relined and contained two more eggs in late May. In early June it was destroyed by a predator (Russell, 1964). At Tikal, El Petén, Guatemala a nest with two eggs was also found in the hollowed top of a palm stump, 1.8 m up (Smithe, 1966).

NESTLINGS

Appearance and development.—While incubation was in progress I disturbed the fifth nest as little as possible, as I wished, above all, to study the care of the nestlings. On my visits to see whether the eggs had hatched, the parent sometimes permitted me to approach within 1 m before she flew. At 12:30 on 24 August both eggs were barely pipped, and 24 hours later they had changed little. By 9:45 on 26 August the nestlings were already dry and the shells had been removed.

The newly hatched manakins were densely covered with grayish brown down about 16 mm long. With the exception of the Bearded Bellbird (*Procnias averano*) described by B. K. Snow (1970) and the Black-faced Antthrush (*Formicarius analis*) (Skutch, 1969), no other passerine nestling of which I know is so well covered with natal down. Resting with heads bent under, the two nestling manakins made a single featureless mass of soft grayish brown, difficult to distinguish from the nest in the deep shade of the palm clump. The nestling's bill was mostly black; oral flanges pale yellow; interior

of mouth yellow; legs and toes plumbeous.

During their first ten days I always found these nestlings resting as when I first saw them, a featureless downy mound that grew larger but otherwise remained unchanged. Neither by gently shaking the nest, moving my hand above it, nor making low sounds could I stimulate these nestlings to rise up with gaping mouths, as many passerine nestlings do. Since such a response in the presence of a predator could have canceled the value of their cryptic aspect, their sluggishness was adaptive, and it probably accounts for the long delays in their acceptance of food from their parent, as will presently be told. Only the slight movements of their breathing revealed that the dark mound of down contained life. However, when I lightly prodded the nestlings with a stick, they squirmed around violently, moving their stubby wings but not revealing their heads, looking like anything but nestlings.

Six days after the nestlings hatched their skins had turned dusky beneath their abundant down. On the body pinfeathers were just sprouting. Those of the remiges had become longer. Two days later the feathers along the sides of the breast and abdomen were emerging from their short sheaths, but the others were still enclosed. When the nestlings were ten days old I found them lying with their heads inclined upward, resting against the side of the nest, instead of turned under. Nevertheless, only the black tips of their bills protruded from the mass of dark down that now filled the nest bowl. Their eyes were at last opening. On this day, when I held a hand above the nest, one nestling raised its open mouth, exposing the yellow lining, and peeped weakly—the only time a nestling gaped to me.

Between 6 and 7 September one nestling inexplicably vanished. When the survivor was 13 days old its body feathers and remiges were quite generally escaping from their sheaths. At 18 days of age the nestling was well feathered. Its upper plumage resembled that of adults, except that the top of its head was much lighter cinnamon-brown or rufescent, as Ridgway (1907) described for *Schiffornis amazonus*. The nestling's body was still shaded by much of its long natal down. To prevent premature departure I did not lift it from its nest to examine its underparts. Now it rested with its tail in front, where the rim was lowest, and its head inward, toward the high rim at the back of the nest, and turned sideways so that it could look out through the gap in the rim, in just the posture taken by its incubating or brooding parent.

Between 7:00 and 14:00 on 15 September, when 20 days old, this young manakin left the nest, apparently spontaneously, as the lining had not been pulled up, as happens when a clinging nestling is torn from its nest by a predator. To the end the downy young manakin blended well with its nest. Its most revealing features were its eyes and cinnamon-brown pileum. If it had kept its head bent under, as when it was younger, it would have continued to be most difficult to distinguish from the dead leaves amid which it sat.

Brooding.—On the morning when the nestlings hatched, their mother continued to brood, watching me, while I arranged a blind about 6 m

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away, a prolonged and somewhat noisy operation, as it was necessary to clear a space to set it amid tangled undergrowth. When I entered the blind in the dim, misty woodland at 5:30 next morning, the adult was already absent. Soon she returned with a small item in her bill, probably fed a nestling while the light was still too dim for me to see well, and settled down to brood. From then until I left at 11:30 she covered the day-old nestlings for five periods, ranging from 9 to 89 minutes and averaging 47 minutes. Although her longest session came at the beginning of the morning, her next longest, 72 minutes, was at the end. The four recesses that I timed in full ranged from 8 to 62 minutes and averaged 25 minutes. She was on the nest 65 per cent of the six hours that I watched, or about as much as the incubating Thrush-like Manakin that we earlier studied.

The parent always entered and left the nest on the side away from the center of the palm clump, where the rim was lowest. She consistently sat with her tail in this gap in the rim, her head toward the high wall at the back, over which she could not see. She might turn her head to the right or the left, but she always maintained the same motionless posture throughout even her longest sessions, looking out through the gap, over her tail and toward the blind, with one big, dark brown eye. Only when about to leave did she turn her head from side to side. She always flew away through the undergrowth, near the ground.

When next I watched the nest throughout the morning of 1 September, the six-day-old nestlings were not brooded. Although I never again saw the parent on the nest on a clear morning, she flew from it in the middle of the afternoon of 11 September, as I approached through the woodland dripping after a hard shower. The usually silent nestling squawked twice when its parent suddenly left it exposed. In the neighboring undergrowth she repeated over and over a song hardly to be distinguished from that of the male. On the afternoon of 14 September I found the nestling, now 19 days old and well feathered, alone in a hard rain that had already continued for over an hour.

Feeding.—When bringing food the parent always approached the nest with great caution. I would first become aware of her as she flew up through the underwood, to alight low on a slender, upright stem, less often on a horizontal branch near the ground. Clinging there she raised and lowered her foreparts and turned from side to side, while she scrutinized her surroundings with large, dark eyes. Often she flew to another perch to continue her survey, and sometimes to several more. Occasionally she voiced the tripartite call while so engaged. Reassured by her careful inspection, she advanced to the nest, often by a circuitous route. Sometimes, possibly because she was distrustful of my blind, she flew away with food in her bill. While the parent was looking around on the nestlings' seventh morning, an Agouti (*Dasyprocta punctata*) walked beneath her nest, paying no attention to it. As the rodent passed the manakin flew back into the undergrowth, but no sooner had it vanished than she advanced to her usual survey post, looked around briefly, then went to the nest.

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To deliver a meal the parent always stood at the front of the nest, where the rim was lowest, with her head inward and her tail toward me. This made it difficult for me to follow the details of feeding, but if I had watched from any other angle I would have seen less. After the first few days the parent brought very large, substantial items, always one at a time, and at long intervals. When the two nestlings were one day old she came with food six times in the first six hours of the day (5:30 to 11:30). After the morning's first feeding she brooded for 89 minutes. As she flew from the nest at the conclusion of this long session, the nestlings gaped and peeped weakly. Nevertheless, when she returned with a green insect 14 minutes later, she ate it herself, then settled down for another long interval of brooding. Apparently the nestlings swallowed the other five items that she brought.

When the nestlings were six days old the parent brought food five times from 5:30 to 11:30. One of the five articles was swallowed by her and another carried away undelivered, with the result that only three were given to the two young in six hours.

When the nestlings were 11 days old the parent brought food to the nest just three times from 5:30 to 11:30. Only the first two of these items were taken by the nestlings. She arrived with the third at 7:15, alighted on the nest's rim, stood there motionless, head turned 90 degrees to the left, holding the food for 55 minutes, then flew off without having offered it to the nestlings, which I did not see gape. This was at 8:10. Through the remainder of the forenoon I failed to see the parent, although once I heard a manakin that was probably she. Despite the nestlings' long fast I could not induce them to open their mouths when I left the blind at 11:30.

When next I watched through the morning, 18 days after the nestlings hatched, only one remained. It was now becoming feathered. In the dim early light the parent arrived with a big green larva, peered around from a vertical stem, then flew off without having visited the nest. Half an hour later she returned and fed the nestling. In the remainder of the morning she brought four more meals. Accordingly, the single nestling received five meals in six hours, the highest rate of feeding that I recorded at this nest.

A five-day-old nestling that I watched in 1942 was fed three times in as many hours of the early morning. The parent of this earlier nestling, and others that I have watched, seemed less shy and suspicious than the one I studied in 1977.

Early on the morning of the day after the nestlings hatched, their parent gave them objects no longer than her small bill, but later in the forenoon she brought, and delivered to them, fairly large green and white larvae. On subsequent days she nearly always brought items so big that I wondered how the nestlings managed to swallow them. Most frequent were long, fat, solid-looking larvae. One day the mother came with a corpulent green insect too badly mangled for identification, as were certain dark and whitish objects that the young received. Although berries are prominent in the diets of

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the smaller, more typical manakins, this Thrush-like Manakin brought no fruit.

Despite infrequent meals the nestlings rarely seemed eager for food. Often two or three minutes elapsed before one took what she brought, and once, as already told, the parent sat holding the food for nearly an hour, then carried it away. The nestlings' slow response, evidently related to the time it took to digest their substantial meals, was consistent with the whole pattern of their cryptic appearance and behavior. By bringing sustaining meals to silent nestlings at long intervals, the manakin reduced the risk of drawing predators' attention to her nest.

Sanitation.—From the first day the parent carried away in her bill the white fecal sacs, which soon became large and heavy. I saw her swallow only a single dropping, when the nestlings were one day old.

At this nest, as at those I earlier watched, I never had two attendants simultaneously in view. As in other members of the family, the female Thrush-like Manakin attends her nest alone.

FLEDGED YOUNG

After the surviving nestling left the nest on 15 September, aged 20 days, it disappeared into the dense underwood. On the following 10 December I heard in this woods, near the site of the nest, a prolonged, mellow, single whistle that was repeated over and over. Unable to surmise which bird it might be, I searched until I found him, perching about 3.5 m up at a considerable distance from the point where I first heard him. I could hardly believe that the brown bird was a Thrush-like Manakin until, after delivering the puzzling single whistle, he uttered an exceedingly faint version of the manakin's tripartite whistle. Soon he flew off beyond sight and hearing. Probably this was the manakin hatched in the nest that I had watched, now three and a half months old, practicing his first songs in solitude. In the dim forest light I seemed to detect yellow at the corners of his mouth.

SUMMARY

A solitary inhabitant of the dimly lighted underwood of humid forests, the Thrush-like Manakin utters a beautiful tripartite whistle so ventriloquial that it fails to reveal the bird's location. Without alighting, it plucks berries and insects from twigs and foliage.

In the Valley of El General five occupied nests were found from late February to August. Each was a bulky cup of large dead leaves, sparsely lined with fibrous rootlets, and situated from 1 to 1.3 m up in a clump of spiny palms or a tangle of vines. In other regions the Thrush-like Manakin nests in the hollow tops of low palm stumps. The usual set is of two eggs. They are incubated by the female alone and hatch in 20 to 21 days.

The nestlings, densely covered with grayish brown down, rest during their first ten days with heads turned under, forming a featureless mass

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difficult to distinguish from the nest. Their behavior accords with their cryptic aspect. They are silent, respond tardily to their parent's arrival with food, and can scarcely ever be made to gape by movements and sounds that elicit prompt reactions from many passerine nestlings.

The parent brooded day-old nestlings about as constantly as they incubate the eggs. After the young were six days old the parent was not seen covering them except when it rained.

The nestlings' meals, substantial but very widely spaced, usually consisted of a single caterpillar so long and corpulent that they could scarcely swallow it. Sometimes they received large mangled insects, but no berries were fed. During the first six hours of the day the parent brought food from three to six times, but some items were carried away undelivered.

One nestling inexplicably vanished and the other left, apparently spontaneously, when 20 days old.

No second parent was ever seen to take an interest in the nest or young.

A young fledged manakin uttered single whistles with little resemblance to the tripartite whistles of adults.



FIG. 7. Sulphur-rumped Flycatcher, *Myiobius barbatus*.

Family TYRANNIDAE
BRIGHT-RUMPED ATTLA

Attila spadiceus

A slender, active, extremely vocal bird, the Bright-rumped Attila is not easily confused with any other bird of Central America except possibly, by novices in bird identification, with the large *Myiodynastes* flycatchers. Over its vast range its plumage is so variable that it has been called the Polymorphic Attila. The Costa Rican forms, with which this account deals, are nearly 19 cm long and the sexes are too similar to be readily distinguished. The head and hindneck are greenish olive with inconspicuous dusky streaks on the crown and nape, and narrow, pale streaks above the eye. The back varies from rufous-brown to brownish olive. The rump and uppertail coverts are light yellow. The grayish brown or brownish olive tail brightens to brownish cinnamon or orange-tawny at the base. The grayish brown wings have lighter spots on the coverts. The pale yellow throat and chest are more or less distinctly streaked with grayish or olive. The lower breast and abdomen are white, passing into pale yellow on the sides and flanks. The moderately long, straight, and rather slender bill is pale at the base, dusky subterminally, with a pale tip. The legs and toes are bluish gray. In a mated pair that we watched for many hours at close range in the northern Caribbean lowlands of Costa Rica, the only difference that we could detect between the sexes was in the color of their irises, which in the male were brighter yellow than in the female. In the southern half of Costa Rica's Pacific slope attilas have red rather than yellow eyes.

The Bright-rumped Attila ranges over continental America from well beyond the Tropic of Cancer in the Mexican state of Sinaloa to western Ecuador, Bolivia, and southern Brazil, and it also inhabits Trinidad. In altitude it extends from sea level up to 1,700 m in northwestern Mexico (Ridgway, 1907), 1,850 m in Costa Rica (Carriker, 1910; and my own records), and to 2,100 m in Venezuela (Phelps and Phelps, 1963). In its many races the Bright-rumped Attila inhabits both rain forests and drier deciduous woodland, as on the Yucatán Peninsula (Paynter, 1955). From the forests where it is most often found it visits nearby plantations with scattered tall trees, shady pastures, older second-growth, and even dooryards and gardens, to forage and sometimes to nest. It forages from the ground to high in trees, but while singing or calling, except near its low nest, it usually remains high and is difficult to detect amid foliage.

Attila is a solitary bird. I have never seen it flocking with others of its kind, and rarely with the mixed flocks that wander through the woodland. Possibly because it is not easy to see in the treetops, I lack evidence that it remains mated after the young of the year become independent. Nowhere have I found it common; but in past years it was moderately abundant in the heavy forests on the Pacific slope of extreme southern Costa Rica

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from the Golfo Dulce up to about 1,200 m. Wherever it occurs it is easily recognized by its slender form, bright rump, long tail flagged up and down, and, above all, by its loud, unmistakable calls.

FOOD

From observations of parents feeding their young, I infer that attilas subsist chiefly upon small lizards and tiny frogs. They also consume a variety of insects and take vegetable food at least occasionally. Except while plucking fruits, those that I have watched foraging were at no great height. Late on a cloudy afternoon in mid-April, while I sat in a highland pasture watching a Blue-throated Toucanet's (*Aulacorhynchus caeruleogularis*) nest, an attila flew out of the forest 100 m away and alighted on a low stump. For about 15 minutes the bird flew from stump to log, always within a meter of the grass wet from the recent shower, to which it from time to time dropped, evidently to catch an insect, frog, or lizard. While it stood on a stump scrutinizing the grass, it constantly wagged its tail up and down through a wide arc. At the same time migrating Swainson's Thrushes (*Catharus ustulatus*) were foraging from the same stumps and logs, and a Western Wood-Pewee (*Contopus sordidulus*) was catching insects from a low stump. Ground-foraging is apparently not rare.

At Los Cusingos one July, during the mid-afternoon break in the rain usual at this season, an attila emerged from the neighboring forest and for nearly an hour hunted over the ground, resting on low rocks, fallen branches, and often on the short-cropped grass over which it hopped with feet together instead of walking. I saw it capture only small items, probably insects and spiders. It was wholly silent.

Occasionally the Bright-rumped Attila joins the birds of many kinds that forage with army ants. One attila accompanied the party of antbirds, tanagers, and other customary ant-followers with which an immature Collared Forest-Falcon (*Micrastur semitorquatus*) was also foraging in the forest at Los Cusingos. Like the other small birds, the attila maintained a respectful distance from the large raptor, whose presence did not greatly inhibit the activities of any of them. Of all these ant-followers, the attila consistently stayed highest, mostly 4 to 6 m above the ground over which the ants swarmed. From time to time it darted swiftly to capture an insect that was trying to escape the ants by crawling up a tree trunk. More rarely it swooped down close to the ground to seize one in flight; but, possibly because the hawk stayed low, I did not see it alight anywhere below the level of my head. All its movements were executed with great dash; the dart that it made to catch an insect often carried it many meters beyond its objective. Sharp, excited notes accompanied its flight. The attila continued with the ants a long while and gathered a rich harvest of insects that they drove up from the ground litter.

On another occasion when the army ants and their avian followers had entered a pasture beside the forest, the attila that accompanied them once

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descended to the ground. If this bird, whose classification is uncertain, is in fact a cotinga rather than an American flycatcher, it is the only member of the cotinga family that I have seen foraging with army ants; most stay too high for this and are only rarely seen near the ground.

Of vegetable foods I have known the attila to eat the arillate seeds of the trees *Alchornea costaricensis* and *Dipterodendron elegans* and the liana *Davilla Kunthii*. Arils, outgrowths from seeds which they partly or wholly cover, are usually rich in oil but poor in starch and sugar. They are highly attractive to birds of many kinds, including some that are mainly insectivorous, who prefer them to nearby berries. Wetmore (1972) reported that in the early morning attilas may drink at shaded stream banks or small forest pools.

VOICE

The attila's loud, clear, assertive notes are unmistakable and often reveal the bird's presence in the crown of a tree where it perches unseen. Chapman's (1929) paraphrase of one of its frequent calls or songs, *beat-it, beat-it, beat-it no-ó-w*, suggests the sense of urgency that this far-carrying utterance conveys. More pensive is the clear, melodious *ooo, weery weery weery weery weery weery weery woo* that I have often heard in Costa Rican mountains. A briefer phrase, frequently associated with this, sounds like *we her her*. Attilas often continue for many minutes to repeat their bright, rhythmic songs, which in Panama have won for this species the name *pájaro gritón*—the vociferous bird (Wetmore, 1972). Even the risk of calling attention to their low nests fails to silence them. The male performs much near the nest and his mate frequently sings while sitting in it, in a voice much like his but usually softer. On short flights from perch to perch, attilas voice sharp, rattling notes. While inspecting a nest site or sitting in the nest, both sexes, but especially the female, deliver, with rapidly moving lower mandible, a long series of low, soft notes, a sort of lullaby suggestive of contentment or maternal affection. Such twittering nest songs are not uncommon in the Tyrannidae. In Costa Rica I have heard loud song chiefly from February to April when attilas are nesting or preparing to do so, but I also have records of singing in July, November, and December.

NEST

When I wrote my earlier account of the Bright-rumped Attila (Skutch, 1971b) I had seen only two Costa Rican nests, both in the same site, and had found a few brief notes on nesting in other countries. Subsequently I examined four more nests in Costa Rica, one of which I could study in some detail. These and a few other nests for which I have adequate data were all low, the highest being only about two meters above the ground. Otherwise the sites differed so widely that it seems proper to describe them in some detail.

At "La Selva," near Puerto Viejo in the Province of Heredia in the Caribbean lowlands of Costa Rica, I found the first nest on 12 April 1967. As I walked

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by a towering surá tree (*Terminalia lucida*) that grew beside a stream at the edge of a shady cacao plantation, a bird with a yellow rump darted out from between the high, wide-spreading plank buttresses. In the deep bay between two of these buttresses was a small shelf, in the angle where they met. Here, only 80 cm above the ground, rested the nest, supported in front by a slender sapling that grew on the great, smooth-barked trunk. This nest was a bulky open cup, composed of dark fibrous rootlets, rachises of compound leaves, and a few pieces of green fern fronds. The lining consisted of slender, curved secondary rachises of the twice-pinnate leaves of the gavián tree (*Pentaclethra macroloba*), mixed with a few rootlets and light-colored fibers. The cupped interior measured 8.5 cm in diameter by 4 cm deep. It then contained four nestlings which flew on 24 April, after which I removed the nest. When I returned to La Selva on 11 March of the following year, a new nest, built in exactly the same spot, already contained an incomplete set of eggs. In the interval an epiphytic begonia had grown up in front of the niche, and one of its large leaves partly screened the nest.

A nest found by Wetmore (1972, and *in litt.*) while walking along the bank of the lower Río Maje in eastern Panama, was evidently in a quite similar situation, but higher "a little over 2 meters above the ground." Built in the bottom of a narrow space in a fork between two sections of a large tree, the cup of dark rootlets held three beautifully marked eggs, far advanced in incubation on 20 March 1950.

My third nest was in a very different situation, 115 cm up in a deep nook amid massed tank bromeliads on a stump in the botanic garden at Las Cruces, near San Vito de Java, Costa Rica, not far from the border of Panama. This site, near a hilltop on which stood an occupied house, was far from any stream. When found on 23 April 1973 it held three well-feathered nestlings, which left the following morning. Almost exactly one year later I found another nest with three feathered nestlings, 1.3 m up on the same bromeliad-covered stump or a similar one nearby.

From time to time over the years attilas have come into our garden at Los Cusingos from the adjoining forest and called loudly, while they flew restlessly from tree to tree around the house. They seemed to be seeking a nest site but usually, after a few days, they vanished. Finally, they nested in a madera negra tree (*Gliricidia sepium*) between the garden and the pasture. This tree had been planted over thirty years earlier as a living fence post and had been frequently pollarded, leaving thick stubs of upright branches, overgrown with mosses, ferns, and a variety of flowering epiphytes. Amid this massed vegetation sheltered nooks offered sites for nests. Little building was needed; after finding or making a depression 2 m above the ground in the matted, slender rootlets of the epiphytes, the attila added a sparse, fibrous lining. After they lost eggs from their first nest in the madera negra in March 1975, the attilas stayed away for three years. In March 1978 they returned and nested in a snug niche beneath a bromeliad, 2 m up in a neighboring madera negra. This nest, close by a gate that

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was frequently used, was about 100 m from the forest to the south and 10 m from tall second-growth woods on the opposite side.

Beebe (1925) recorded *Attila* (apparently *spadiceus*) as "nesting in hollow trees" in British Guiana (now Guyana). Similarly, Belcher and Smooker (1936) found a nest of *A. spadiceus* in "a hole in a tree." It is not evident from these brief accounts how deep or well enclosed the hollow or hole was. The six nests that I have seen were in nooks or niches from which the attila could look out, and be seen from in front, while she incubated; none was in a deep cavity that completely concealed the sitting bird, such as woodpeckers make and *Myiarchus* flycatchers occupy. In Trinidad a Bright-rumped Attila's nest was 1 m up "on the side of a low bank" (French, 1973). Such a site is apparently not unusual in the genus *Attila*, for in Brazil the Gray-throated Attila (*A. rufus*) builds a bulky nest in a hollow, or short tunnel, in banks above water (Euler, 1900, cited by Mitchell, 1957).

Although all the occupied nests of the Bright-rumped Attila of which I have knowledge were not more than 2 m above the ground, possibly at times the bird chooses a higher site. In the middle of the morning of 3 December 1947, while I resided in a narrow clearing in heavy lowland forest near the Golfo Dulce in southern Costa Rica, I watched a pair of attilas that were obviously interested in such a site. In a niche amid vines and epiphytes, well up on the trunk of a middle-sized tree at the forest's edge, sat one of these birds, pouring forth a continuous stream of low, soft notes. Its posture and the character of its utterance reminded me strongly of a flycatcher choosing a place for its nest. After this song had continued for several minutes the attila's mate came and perched close beside it. Then they moved off together. No nest had been started here by the month's end.

The few observations that I have on nest construction suggest that only one sex, doubtless the female, builds. Soon after sunrise on 11 April 1964, in the highland pasture where I watched the attila foraging in the grass, one of these birds flew out of the forest and alighted on a log. She plucked small pieces of fibrous roots of epiphytes from the surface of the log and continued until her bill held a large sheaf of them. After a minute or two on the log, within a meter of the ground, she flew back into the forest with the rootlets. All this while another attila, probably her mate, sang loudly and melodiously from nearby trees; from other parts of the forest came the answering songs of other attilas, making a far-flung chorus. I waited in vain for the bird to return for more rootlets, and I searched fruitlessly for a nest.

The nests amid the mosses and roots of epiphytes in the madera negra trees close by our house required little additional material, and I saw little building. Early one morning I watched the attila pull rootlets from the trunk of a neighboring tree. At the second of these nests a bird brought five billfuls of material in the 20 minutes from 7:05 to 7:25; but continued watching on several mornings failed to disclose another such concentrated effort. While one gathered material, or sat for minutes arranging the nest,

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the other member of the pair did nothing but sing loudly. Often one or the other rested in the nest space, or a similar nook nearby, uttering the nest song or louder notes. Obviously these noisy birds were not afraid of revealing the situation of their nest by their voices.

EGGS

At the second nest in the madera negra I found the first egg a week after I noticed an attila building there. Two days elapsed between the laying of the second and third eggs, but only one day between the third and fourth. At another nest the fourth egg was laid two days after the third. One egg was laid before 7:00 in the morning; another between 8:20 and 11:00. In all six of the nests, including two in the Caribbean lowlands, two on the Pacific slope at 750 m, and two on the Pacific slope around 1,200 m, the eggs were laid in March, beginning in the second week. Each of three nests contained four eggs; one, in which the set may not have been complete, had three eggs. Two other nests had each three feathered nestlings, and may well have had four eggs. As already told, Wetmore's nest in Panama held three well-incubated eggs on 20 March. Russell (1964) reported, without details, a set of four eggs found at Cayo, British Honduras (now Belize) on 9 April.

The eggs are glossy, dull white to pale buff or pinkish buff, marked, heavily in a wreath around the thicker end and more sparingly elsewhere, with large and small spots and blotches of dark brown, grayish brown, bright cinnamon-rufous, and pale lilac. In coloration these eggs resemble those of certain American flycatchers more closely than such cotingas' eggs as I have seen, which had a buffy gray or grayish brown ground color. The measurements of 10 eggs in Costa Rica average 23.5 by 18.9 mm. Those showing the four extremes measured 25.0 by 19.4 and 22.6 by 18.4 mm.

INCUBATION

Only the female incubates. At the second nest in the surá tree, I found her covering three eggs at 11:20 and she was still on the nest when I left an hour later. She did not complete her set of four eggs until the following morning. Five days later, on 18 March, my son and I alternately watched this nest from a blind from daybreak until the light grew dim at 17:40. The attila first left her eggs at 5:38 and she returned for the night at 17:14. In this interval she was absent only six times, for periods of 26, 45, 55, 31, 60, and 13 minutes. The five sessions which alternated with these recesses lasted 63, 82, 106, 111, and 104 minutes. The day was clear, except for a five-minute shower in the early afternoon. Although this female incubated with great patience, her long sessions were often followed by long absences, with the result that she covered her eggs only 67 per cent of her active day. On the cloudy morning of 26 March she was absent five times, for 14, 32, 18, 26 and 37 minutes, with intervening

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sessions of 49, 36, 60, and 76 minutes. Now she incubated for 63.5 per cent of the morning.

Ten years later, on the opposite side of Costa Rica, the attila in the second nest in the madera negra tree incubated in much the same way. I watched this nest from noon until nightfall on 20 March, and from dawn until noon on the following day. Treating the two half days as one whole day, she first left her nest at 5:53 and returned for the night at 16:33. In her active period of 10 hours and 40 minutes she took five recesses, beginning at sunrise with one that lasted 13 minutes and followed by others of 34, 43, 50, and 39 minutes. Her sessions, of which the longest occupied the second half of the forenoon, continued for 62, 33, 184, 71, and 102 minutes. She was in the nest for 71.5 per cent of her active day. When I next watched this nest, throughout the overcast morning with intermittent sunshine of 1 April, this female was more restless. She left her eggs six times, for 19, 8, 6, 14, 5, and 64 minutes. Her sessions lasted 92, 21, 55, 81, and 32 minutes. She sat in her niche for 70.7 per cent of the six hours and 37 minutes that elapsed from her first departure at 6:00 until she returned to her eggs at 12:37, when I ended my watch.

The behavior of these two pairs of attilas, separated by a high mountain barrier, was similar. Both females permitted a close approach before they left their eggs; sometimes I could almost touch them. The female in the surá sat watching while we set or removed the blind 10 m in front of her. I did not use a blind to study the nest in the madera negra but sat on the hillside above it, 30 m away, using binoculars. Each of these females was escorted by her mate every time she ended her recess. At the surá tree the female, returning from an outing, flew back and forth among the cacao trees in front, often in company with her mate, one or both of them singing loudly and voicing high, sharp, insistent notes. Of a sudden the female would start toward the nest from a low perch in a cacao tree, and her mate would accompany her closely, as though racing to get there first. While she shot in between the plank buttresses to the nest, he veered aside just in time to avoid striking them.

At the madera negra tree the returning female alighted in neighboring shrubbery. After flying back and forth she darted toward the nest with her mate pursuing closely. As she entered he shot past the tree, turned in the air, and went back to the shrubbery. Such spectacular escorting is practised chiefly by males who do not share incubation with mates who sit in closed nests, holes, or crannies, including euphonias (*Euphonia*), tody-flycatchers (*Todirostrum*), and Black-faced Grosbeaks (*Caryothraustes poliogaster*). Once the male attila at the madera negra tree varied his escorting by sitting in an empty niche and giving a prolonged nest song while his partner settled on her eggs higher in the same trunk.

The female attilas sat in their niches facing outward or sideward, never inward. At intervals while incubating each gave the nest song, a long sequence of subdued notes that suggested contentment. Sometimes she sang more loudly, answering her mate with a song similar to his, but at other times

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his voice elicited the nest song. Early one morning the female in the madera negra tree spent much of her session picking from the nest minute objects that were probably ants. At this nest the male often remained among the neighboring shrubbery, guarding. With clacking bill he repeatedly tried to chase away a Buff-throated Saltator (*Saltator maximus*) which had come too near; but the larger bird, that meant no harm, refused to be intimidated. Later, his threatening bill drove away a resident Garden Thrush (*Turdus grayi*) and a migrating Swainson's Thrush (*Catharus ustulatus*).

Thirty-eight hours after I first detected a minute fracture of the shell, an egg hatched in the madera negra tree, at about 7:30. The other three eggs hatched in the afternoon of the same day, the last after 17:00 when I removed the large part of an empty shell that had slipped over it, impeding the hatchling's escape. Other shells had been promptly removed by the female. At this nest the incubation period was 18 days and a few hours. At the earlier nest in the surá tree the incubation period was at least 18 days and may have been somewhat longer, for the egg that failed to hatch could have been the last to be laid.

NESTLINGS

Beginning of feeding.—At 6:40 on 4 April 1978 all four eggs in the madera negra were pipped. At 7:30 I began a continuous watch. At 7:35 the female rose up in the nest and carried away a shell. In a minute she returned to brood for the next 40 minutes. When she left I inspected the nest and found one nestling, not yet dry. After a 10-minute absence she returned, escorted to the nest, as usual, by her mate, but she did not feed the nestling. For the next half hour she sat restlessly, often rising to poke down into the nest. Then she went off for seven minutes and found what appeared to be a tiny lizard. For several minutes she tried to make the nestling take its first meal, while the male flew repeatedly past the nest, his curiosity evidently aroused by the change in his mate's behavior. Thus, the female started to feed the first nestling about one and a half hours after it hatched.

After several more sessions of brooding the female, at 11:56, again brought food, another small lizard. For several minutes she tried without success to give the nestling its second meal, then ate the lizard herself. When I left at 12:35, the male had not yet brought food, or even looked into the nest, although he had several times escorted the female to it, and while sitting she had called much. Evidently her voice did not convey to him the information that he had become the father of a nestling that needed food.

At 16:00, after the second nestling hatched, I resumed my vigil. At 16:18 the male appeared with a small lizard. He hesitated near the nest, but finally gave it to the brooding female, which passed it to a nestling. Whether this was the first meal he brought I could not tell. He had started to feed the nestlings between five and nine hours after the first egg hatched. Other male birds that I have watched have begun to feed much more promptly

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(Skutch, 1976). The attila's considerable delay resulted from his failure to make periodic inspections of the nest to which he so often escorted his incubating partner. Probably he was led to bring food by seeing her do so.

During the remainder of the afternoon, while the last two nestlings were hatching, their father brought three more tiny lizards; their mother came with another lizard and one unrecognized item. Thus, only a few hours after they hatch, nestling attilas receive the lizards which, becoming bigger as they grow older, will be the mainstay of their diet. Both parents tried, with low twitters, to coax the hatchlings to swallow their first meals. When they failed the mother ate the food, whether she or her mate had brought it.

Feeding of older nestlings.—In five hours of the morning of 3 April 1968, three three-day-old nestlings in the surá tree were fed only five times, by both parents. Their meals included two small lizards and a little frog.

On 8 April 1978 the four nestlings in the madera negra, now in their fourth day, received a total of 13 meals in the first five hours of the morning. Both parents brought this food, but I could not always determine their sexes. Each of eight meals consisted of a small lizard, one of which was an *Anolis* with yellow gular pouch extended; two appeared to be mangled insects; and three meals consisted of unidentified objects.

Soon after the foregoing observations were made both of these broods were lost to predators. For the care of older nestlings we must turn to the first nest, discovered in the surá tree after the eggs had hatched. From 14:00 to 17:30 on 12 April 1967 the four newly-found nestlings, estimated to be six days old, received nine lizards, one insect, and an unidentified item, making 11 meals in 3.5 hours. On 15 April, from 6:00 to 12:00, these four nestlings were given 12 lizards, three insects, and one unidentified item, a total of 16 meals in six hours. On 23 April, from 5:45 to 10:45, the same nestlings, now well feathered, were fed 16 times in five hours. Tiny frogs had now replaced lizards as the nestlings' main food; on this morning they received ten of these and only five lizards. A parent never brought more than one item at a time, held conspicuously in its bill. On this morning the male was credited with eight feedings, the female with five, and on three occasions we did not see the parent's eyes well enough to recognize its sex. Sometimes when we visited the nest between our long watches, we found 5 or 8 cm of lizard's tail projecting from a nestling's mouth. At times their mother entered the nest to incubate or brood with a tail projecting from her mouth.

Dennis Paulson watched from the blind and identified the small brown lizards most frequently seen in the parents' bills as adult anoles (*Anolis limifrons*). Less often the parents gave their brood a shiny, short-legged lizard (*Lygosoma cherriei*). Both kinds of lizards were abundant in the cacao plantation at La Selva, where we sometimes saw an attila plunge down into low weeds to seize one of them, or an insect. Lizards were always carried with the head grasped in the bird's bill, the body hanging limply

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to one side. The lizards brought to the very young nestlings in the madera negra tree were too small to be identified.

At all the nests that we watched, a parent arriving with food did not proceed directly to the nest but spent some time flying from branch to branch of the cacao trees or shrubbery in front of it. Sometimes the bird barely touched a branch, then flew off to alight on another; sometimes it delayed on a branch for nearly a minute, or more rarely for several minutes, wagging its tail up and down the while. The male tended to procrastinate in this manner longer than the female, and often he called in a loud, mellow voice, while she was usually silent. These changes of position, before they flew to the nest, should have helped the parents to detect lurking predators. If the female happened to be brooding when her mate came with food, he delivered it to her, and she rose up to pass it to a nestling. After feeding, the female at the surá tree sometimes delayed for several minutes, standing on the nest's rim, tail outward. Once, while she rested so an Agouti (*Dasyprocta punctata*) ran noisily beneath the low nest, but she did not budge. This big, wholly terrestrial, vegetarian rodent was not a threat to her nestlings.

Both parents removed droppings, at first swallowing them but, after the nestlings were older, carrying them away in their bills.

Brooding.—During the five hours from 6:15 to 11:15 the three-day-old nestlings in the second nest in the surá tree were brooded four times, for intervals of 28+, 20, 74, and 62 minutes—a total of 184 minutes. The intervals of exposure were 8, 21, 65, and 22 minutes. During five hours on their fourth morning the nestlings in the madera negra were brooded only twice, early in the morning for 94 minutes, and in mid-morning for 10 minutes. From 14:05 to 17:27 on the day the first nest in the surá was found the still-naked nestlings were brooded for 46, 9, 17, and 10 minutes, and left exposed for intervals of 53, 18, 19, and 30 minutes. Three days later, when these nestlings had sprouting pinfeathers, they were brooded only once in the course of the morning. When a shower began, their mother covered them; but after sitting only six minutes she left, long before the rain stopped. Thus, the time devoted to brooding, which at first was comparable to that spent in incubation, decreased very rapidly.

Defense of nestlings.—When the eggs in the madera negra were about to hatch the female did not leave them until I approached within arm's length. Then, while I inspected the nest, one parent repeatedly darted close above my head, uttering sharp notes and clacking its bill—behavior I had not previously witnessed—while the other perched nearby, uttering loud, clear notes. Until the nestlings vanished six days later these vigorous, noisy feints of attack were repeated whenever I visited the nest. A Cinnamon-bellied Squirrel (*Sciurus granatensis*) was chased away by diving at it with clacking bill.

One morning, just as my son was replacing me in the blind at the surá nest, two attilas fought in the cacao tree in front. Interfering foliage made it difficult to follow the combatants, but they chased each other around

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and sometimes seemed to seize each other. Feathers drifting down revealed the severity of the conflict. Later we saw another fight, between a parent bringing food and another attila. Apparently, the resident pair was resisting an intruder. The cotingas that I know are pacific birds, whose differences are settled by vocalizations and feints. If the attila indeed belongs to this family, this was the fiercest conflict between cotingas that I have seen. I have, however, on rare occasions watched equally intense encounters between flycatchers, especially species of *Elaenia*.

Development.—Newly hatched attilas bear on head and back tufts of fairly long, gray down that are paler at the base and tip. Although rather abundant for a passerine bird, this natal down leaves much of the pink skin exposed. Interpterylar down is lacking. The eyes are tightly closed. The bill, interior of mouth, and flanges at its corners are bright yellow or orange-yellow. The bill bears a minute egg-tooth. The legs and toes of the madera negra nestlings were pale yellowish, but those of the surá nestlings were pale flesh-color. The birds peeped softly. All these young attilas that I had seen as hatchlings were taken by predators when a few days old.

For observations on the later development of nestlings I am dependent upon those in the first surá nest, which I first saw when the pins of their remiges were a few millimeters long, but those of other tracts had not yet erupted from the skin. I estimated their age to be six days. Four days later pinfeathers were sprouting on body and head, and those of the remiges had grown long. The eyes were open. A week after I found these nestlings their plumage was expanding. Pushed up on the ends of the growing feathers, the tufts of natal down looked like little pale stars, or the pappi of composite seeds, sprinkled over crown and back. A little interpterylar down had developed between the feather tracts. When the estimated age of these nestlings was 16 days they were well feathered and resembled their parents in coloration. Usually I found them facing inward, toward the surá trunk that supported their nest.

As in many other suboscine birds, the voices of these nestlings developed precociously. When their eyes had opened, but before any feathers had expanded, I heard them calling *beat-it, beat-it*, in a clear voice, much like that of the adults but weaker. Soon their infantine voices could reproduce much, if not all, of the adults' repertoire, which they did most freely when they heard a parent approaching with a meal. On 23 April they preened much and vigorously flapped their wings, now with expanded remiges. In the course of these exercises one almost fell from the nest, but saved itself by clinging to the outside and climbed back to the interior. At 17:00 on this date all four nestlings were still present but by 7:00 next morning they had gone. They left the nest 12 days after I found them, when they were about 18 days old.

Young after leaving the nest.—After the four fledglings left the surá tree on 24 April the family was very noisy. For a few days they stayed in the cacao plantation beside which they had been raised, then they moved farther off. As late as the first week of June a vociferous family of attilas still

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wandered through the forest and adjacent clearings. Now I could distinguish the young from their parents chiefly by their brown rather than yellow eyes. I watched a family, possibly the one whose nesting I had studied, visit a tree of *Alchornea costaricensis* growing beside a forest stream. The small green pods of this tree of the spurge family were opening, exposing hard little seeds covered by thin, bright red, fleshy arils, which attracted many birds, from big toucans and oropendolas to diminutive manakins and honeycreepers. Although the young attilas were full grown and fed themselves, they received many of the red seeds from their parents.

A LATER BROOD?

After the six-day-old nestlings disappeared from the surá nest on 6 April 1968 I searched through the cacao plantation for a replacement nest between the plank buttresses of the many similar surá trees, but I found no other nest. After the four-day old nestlings were taken from the madera negra nest on 9 April 1978 the parents continued for several days to frequent our garden, singing much. Then, for a number of additional days I heard them in the neighboring forest. They wandered widely; whenever I searched for a nest in one area where they had been singing, I heard them in another part of the woods. Finally, they passed beyond my ken. This has almost invariably been my experience with birds of tropical rain forest; when they lose a nest it is useless to search for another nearby. I have no evidence for second broods in this species.

SUMMARY

Over an enormous range, the Bright-rumped Attila inhabits both rain forests and drier deciduous woods, from sea level up to about 2,000 m. From the woodland it frequently enters neighboring clearings to forage and to nest.

Often hunting over the ground as well as in trees, it captures many small lizards and frogs. Its diet includes insects, small fruits, and arillate seeds. Occasionally it joins mixed flocks that follow army ants.

A most vociferous bird, attila utters a variety of loud calls that are sometimes sharply assertive, sometimes more softly melodious. While inspecting nest sites or sitting in the nest, both sexes voice a prolonged series of soft notes—the “nest song.”

The open, cup-shaped nest is built in a niche or nook, often in a shady clearing near or even distant from forest. Sites included deep embayments between plank buttresses of great trees, crannies amid epiphytes on pollarded trees, and amid massed bromeliads on a stump in a garden. The heights of seven nests ranged from 80 to 200 cm. Only the female was seen building.

In Costa Rica three or four eggs are laid in March.

At two nests only the females incubated, taking sessions which ranged from 21 to 184 minutes and covering their eggs from 63.5 to 71.5 per cent of their active day. As the female returns to her nest her mate escorts

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her so closely that he seems to try to reach it first. At two nests the incubation period was 18 days.

The young hatch with fairly long, rather abundant down that fails to cover their pink skins. Their earliest meals consisted of tiny lizards; these reptiles, becoming bigger as the nestlings grew, were at widely separated nests the principal food. Insects and small frogs varied their diets. Although he does not brood, the male takes a large share in feeding and defending the young. One male started to feed between four and nine hours after the first egg hatched.

Even before they are feathered the nestlings, as in other suboscine passerines, repeat the characteristic calls of their parents.

When, at about 18 days of age, the young leave the nest they resemble their parents in plumage but have brown rather than yellow eyes. Flying young are fed while they wander widely with their parents as a vociferous family.

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Myiarchus tuberculifer

The Dusky-capped Flycatcher is readily distinguished from other species of its confusing genus by its smaller size and darker crown, as well as by its voice. Ranging from about 15 to 18 cm in length in its many races, this slender flycatcher has the top of the head brownish olive to sooty brown or even black, usually much darker than the olive or greenish olive back and rump. The light gray of the throat and breast blends with the pale yellow of the abdomen and undertail coverts. The feathers of the grayish brown tail have paler, often cinnamon-rufous, margins. The dark grayish brown wings are also marked with buffy brown and cinnamon-rufous. The eyes are brown and the bill, legs, and toes are dark.

This widely distributed flycatcher ranges from southern Arizona and New Mexico (where it is known as the Olivaceous Flycatcher) through Mexico, Central and South America to Bolivia, northwestern Argentina, Paraguay, and southern Brazil. At both extremes of this immense range it is migratory, but within the tropics it appears everywhere to be permanently resident. Altitudinally, it is found from the lowlands up to about 2,000 m in Venezuela (Phelps and Phelps, 1963) and 1,800 m in Panama, Costa Rica, and Honduras (Monroe, 1968). Farther north it extends higher, at least in summer. In western Guatemala I occasionally met it at about 2,450 m and it has been recorded as high in Mexico (Miller *et al.*, 1957). In the Huachuca Mountains of Arizona it is found at 2,300 m but is most abundant below 1,850 m (Bent, 1942). Highest of all lives the race *M. tuberculifer atriceps*, which in the Andes of Ecuador, Peru, and Bolivia is found at altitudes ranging from 750 to 3,400 m (Lanyon, 1978).

As tolerant of habitats as it is of latitudes and altitudes, the Dusky-capped Flycatcher inhabits semi-arid as well as extremely rainy regions. It frequents

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forest edges, light or open woodland, shady plantations, clearings with scattered trees, and similar situations. In dense rain forests it prefers the canopy where, if silent, it is likely to pass unnoticed. Largely insectivorous, it plucks much of its prey from foliage, but it seizes some on aerial sallies, and occasionally it descends to a low perch, such as fallen brush, from which it drops to the ground to seize grasshoppers, spiders, and other small creatures. Bent (1942) lists most of the 20 kinds of insects found in the stomach of an "Olivaceous Flycatcher" in Arizona. Although vegetable food does not enter largely into the diet of Dusky-capped Flycatchers, I have seen them eat the small arillate seeds of *Casearia sylvestris* and Wetmore (1972) recorded that they come regularly to fruiting trees to gather berries in company with other forest birds.

Dusky-capped Flycatchers appear never to flock. They usually avoid the high, exposed perches and long aerial sallies that many of the larger flycatchers prefer. Typically they remain within or close to sheltering foliage, where they readily escape detection except while they call or sing, which they rarely do except in subdued light. After the breeding season each sex appears to go its own way, but in El General I have found pairs in early January and rarely in December, long before nesting begins.

This flycatcher's usual note is a prolonged, plaintive, subdued whistle or whine, which may be written *wee-ee-ee* or *wheeer*. At daybreak in the nesting season Dusky-capped Flycatchers, probably always males, deliver a twilight song that continues with scarcely a pause for many minutes and is not easily confused with the utterance of any other bird that I know. Among its component notes are a short, sharp, whistled *whit*, a long-drawn, plaintive, whistled *wheeeu*, and a whistled, cut-off-short, *we-du*. These notes are combined in various sequences, with occasionally the interjection of a harsh trill. From at least Guatemala to the Canal Zone, despite racial variation, the Dusky-capped Flycatcher's dawn song has much the same character. I have only once heard this performance after sunset. Frequently I have heard it on cloudy afternoons, when it included many long, harsh trills.

NEST BUILDING

Despite the abundance of Dusky-capped Flycatchers in many parts of their vast range, their breeding habits are poorly known. Even in Arizona, where the most nests appear to have been found, no detailed study of their nest life seems to have been made. Everywhere this flycatcher nests in a cavity, usually in a tree, which may be high or low. In southwestern United States most nests were from 6 to 15 m up, although one was as low as 1.2 m (Bent, 1942). In Trinidad Belcher and Smooker (1937) found eggs in two successive years in the same hole, about 4.5 m up in a dead stump near a forestry plantation. In my earlier account of this species (1960) I reported on one nest that I found near the Caribbean coast of Honduras in 1930, and two in the Motagua Valley of Guatemala in 1932. Two of

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these nests were in hollows in decaying fence posts, the third in a deep cavity in the broken-off end of a small, leaning tree on a steep, scrubby hillside. These three nests were from 1 to 1.7 m above the ground. In the leaning tree the eggs rested 18 cm below the opening, at the bottom of a hollow so narrow that only with great difficulty could I insert my hand to reach them with my finger tips.

Other studies left little time for watching any of these three nests in northern Central America. For well over four decades, passed mostly where Dusky-capped Flycatchers are at least not excessively rare, I have been trying to fill gaps in our knowledge of their life history, without brilliant success, as the six additional nests that I have found were either inaccessible or failures. Nevertheless, in spite of the incompleteness of information on this species, it appears desirable to publish what I have learned.

Part of the difficulty of finding Dusky-capped Flycatchers' nests comes from the erratic way that they build them and the secrecy with which they later attend them. Three of the six nests that I have found in the Valley of El General were in old, dying *Inga* shade trees in a small coffee plantation near our house, at heights of about 6 to 8 m. Although I passed much time in this *cafetal*, watching other birds, and for weeks suspected that Dusky-capped Flycatchers were nesting there, they did not reveal their nest's location to me until 24 May 1959 when the nestlings were already well grown, to judge by their very frequent meals. Even repeated knocking on the trunk had failed to make an incubating or brooding parent emerge from the hollow end of the thick, broken-off branch in which the nest was hidden. Two years later the flycatchers again nested in this coffee plantation, this time in a hole made by Golden-naped Woodpeckers (*Melanerpes chrysauen*) the preceding year. The top of this chamber had broken off so that the parent flycatchers could enter either through the woodpeckers' doorway or through the open end of the stub. Although I failed to find this nest before the eggs were laid, I did discover it before they hatched.

On 12 April of the following year, 1962, I noticed a Dusky-capped Flycatcher breaking twiglets from trees or vines and carrying them into the hollow end of a thick, nearly upright branch of one of these old, dying *Inga* trees. Before I could learn how many individuals were engaged in this occupation, the pair flew away. On the next three days I watched much without seeing a bird at work. But at about 9:20 on 16 April a low, mournful whistle drew my attention to a flycatcher in the branches above me, carrying a feather that she took into the hollow stub. By 9:55 she had taken 15 billfuls into the cavity. By 10:20 she had brought only two more billfuls, making a total of 17 in the hour. In the following 15 minutes, she made five more trips to the nest, after which she stayed away.

Only one member of the pair, whose tail feathers of unequal length readily distinguished her from her mate, took materials into the nest. These were usually chicken feathers, white or at least light-colored, which were carried singly, or often many bunched together. One feather, carried alone, was nearly as long as the bird that held it. One load consisted of a feather

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and a slender twig or length of vine, grasped tightly together. On several visits the bird brought a sheaf of fine, light-colored fibers or possibly seed down. Once she carried the base of a grass plant, with short roots attached. Occasionally she voiced a low, sad whistle while holding material in her bill. Not shy, she went about her work while I stood in plain view. Her mate was mostly out of sight. I watched most of the following morning without seeing the flycatcher at work. As far as I could learn she did not lay eggs in this cavity.

Thirteen years later, in mid-April of 1975, I again found a Dusky-capped Flycatcher building. This time the site was the hollow end of a strongly leaning, decaying stem of a timber bamboo, about 10 m up, just inside a great clump of these stout bamboos at the forest's edge. Although I could not distinguish the sexes, only one member of the pair appeared to bring material. Usually she came with a loose mass of fine fibers, half as big as herself. On other trips her load was an equally bulky fluff of seed down, evidently from a ceibo tree (*Bombax Barrigon*) about 120 m distant. On each visit she dived with her contribution into the wide opening in the top of the bamboo stem. Sometimes she emerged with bits of down sticking to her bill, and tried to remove them by rubbing it against a perch. A low *weer* was the only note I heard from her. I first found her at work at 7:35 on 18 April; in the next 20 minutes she brought material nine times. Later that morning she came with eight billfuls in half an hour. Continued watching revealed only sporadic building. Her mate sometimes perched nearby with empty bill. Again I failed to find the flycatcher incubating in this inaccessible nest.

The only accessible nest that I have seen south of Honduras was 1.8 m up in the end of a horizontal length of timber bamboo, part of a trellis made for a chayote vine (*Sechium edule*) that had died. It rested upon living posts of madera negra (*Gliricidia sepium*) close by a woodshed. The internal diameter of the bamboo was 7.5 cm, and the eggs lay 35 cm from the open end, close to the first transverse wall. The weathered bamboo had narrow fissures that admitted light to the nest. Among its ingredients were downy feathers and fragments of snake skin.

As is evident from the accounts of building, the nests are made of very diverse materials, among which feathers, soft fibers, and seed down predominate. A nest in Guatemala likewise contained snake skin, which had fallen into detached scutes. In the Guatemalan nests I also found hairs of horses or cows. A nest from the Huachuca Mountains, Arizona was composed of such varied materials as straws, grasses, weed stems and tops, dead leaves, strips of bark, cow's hair, fur, and feathers; in the center it was lined with a felted mass of rabbit's fur (Bent, 1942). A nest in Trinidad was composed of dried weed stems and moss and was lined with black, horsehair-like fibers strongly woven together (Belcher and Smooker, 1937). A nest found at about 1,750 m in the Sierra Madre del Sur, Oaxaca, Mexico, in a broken-off stub of a dead tree in cloud forest, was made wholly of animal fur and is illustrated by Rowley (1966).

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EGGS

Each of the two nests in Guatemala contained four eggs, which hatched on 27 April and 5 June. The nest in Honduras held three nestlings, which left on 26 May. From British Honduras (now Belize) Russell (1964) reported two sets of four eggs, found on 21 April and 10 May, in cavities 45 cm and 11 m above the ground. The single accessible Costa Rican nest held three eggs that were evidently laid at the end of March, as they hatched on 12 April. In Trinidad two sets of three eggs were found on 17 April and 15 June. Rowley's nest in southern Mexico held four eggs on 8 June. In Arizona, where Dusky-capped Flycatchers appear to lay chiefly in June, their set consists of four or five eggs. The few available records reveal the well-known "latitude effect": three eggs in Trinidad and Costa Rica, four in northern Central America and southern Mexico, and four or five in the extreme south of the United States.

Eggs that I found in Guatemala were dull white, heavily blotched and speckled with chocolate, chiefly in a wreath around the thicker end. Elsewhere the markings tended to be irregular longitudinal streaks, but on one egg they were dots. The measurements of eight eggs average 20.0 by 15.0 mm. Those showing the four extremes measured 20.6 by 15.5 and 19.1 by 14.3 mm. The eggs in the single accessible Costa Rican nest could not be removed without risking breakage.

INCUBATION

From a blind set in the woodshed I watched the nest in the horizontal length of bamboo throughout the morning of 5 April and the afternoon of 6 April, thereby covering all hours of the day, in about the middle of the incubation period. Only the female incubated. She first left the nest in the dim light at 5:37, when a squirrel hopped along the bamboo that held it. She entered for the night at 16:51, an hour before it grew dark. In the afternoon I missed one of her sudden, swift departures from the end of the bamboo, so my record covers only 10 hours of her active day. In this interval she incubated for 13 periods, ranging from 5 to 68 minutes and averaging 24 minutes. An equal number of recesses ranged from 13 to 41 minutes and averaged 22.7 minutes. She was in the nest for 51.4 per cent of her active day. Her longest sessions, lasting 68 and 53 minutes, were in the early morning, when the bamboo was in shade. The next longest, 49 minutes, came in the late afternoon, when it was again shaded. Her recesses showed less variation but tended to be somewhat longer in the early morning and in the afternoon. Her low constancy of 51.4 per cent is not unusual for small flycatchers.

From time to time the incubating female sang a rapid sequence of low, soft notes, a sort of lullaby, such as nesting flycatchers often sing. Usually she sang so when her mate was nearby. Once, when he alighted on a twig where it was unlikely that she could glimpse him through a crack in the bamboo, she started to sing and continued until a few seconds after his

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departure. She also twittered softly when a Rufous Mourner (*Rhytipterna holerythra*) and, later, a Garden Thrush (*Turdus grayi*) alighted on the bamboo above her; evidently she mistook them for her mate. But the Blue Ground-Doves (*Claravis pretiosa*), that repeatedly stood on the bamboo to preen in the sunshine, failed to elicit the song; probably she could detect the difference between the sound of doves and that of passerine birds alighting upon the hollow bamboo. Aside from these nest songs she came and went in silence, except once when she brought an insect, called twice, then entered and sang a nest song, evidently anticipating the nestlings. They did not hatch until a week later.

The mate of this female was not very attentive. On only two of her 13 returns to the nest did he accompany her, and I saw him near the nest only thrice more during my watches. With one possible exception he did not look into the hollow where the nest was hidden.

In addition to the mourner, the thrush, and the doves, to none of which the flycatchers paid any attention, the bamboo was visited by a small, shiny lizard (*Leiopisma cherriei*) which, while the female was absent, went part way into the nest cavity but promptly left. Early in the morning I glimpsed a large mica (*Spilotes pullatus*) in a small tree with branches which crossed the bamboo that contained the nest, but the snake, an insatiable predator on eggs and nestlings, vanished before I could reach it.

While incubation was in progress in one of the high, inaccessible nests in the *Inga* trees, I watched for 6.5 hours. The female's 12 sessions ranged from 2 to 35 minutes and averaged 17 minutes. Her 12 recesses varied from 8 to 35 minutes and averaged 15 minutes. She incubated for 53.1 per cent of my observation periods. Her nest in an old woodpecker hole with a broken-off top had two entrances. She used both, nearly always going in through the top and leaving through the round doorway in the side. Sometimes in one rapid movement she flew down from high in a tree into the open top of her chamber, so that her entry was easy to miss. Once she carried a billful of feathers into the nest, and once a small insect, evidently anticipating the nestlings. With clashing bill she chased away a Streaked-headed Woodcreeper (*Lepidocolaptes souleyetii*) that was climbing over her nest tree. I saw the flycatcher which was probably her mate only once, when he perched about 10 m from the nest. He did not come closer. As far as I know, in no species of the Tyrannidae does the male incubate.

NESTLINGS

At 15:30 on 12 April I found that all three eggs in the bamboo had hatched since 14:00 on the preceding day, and the shells had already been removed. After my inspection the female brought food. Then, while I stood nearby in plain view, the male arrived with a small dragonfly, wings still attached. He hesitated to approach the nest. When, finally, he reached the entrance, he collided with his mate coming out and flew up into a tree. Then he alighted several times on a twig just above the entrance.

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When at last he approached it, a White-fronted Dove (*Leptotila verreauxi*), alighting just then on the bamboo, caused him to retreat once more. When, after another delay, he went again to the entrance, he no longer had the dragonfly but a moth that he had just caught. After another withdrawal he went halfway in and made a purring sound, as though calling the hatchlings to come and take the insect from him which, of course, they could not do. On his third attempt, however, he vanished into the darkness of the cavity and promptly emerged without the moth, which evidently a nestling had taken. Thus, no more than 24 hours (including the night) after the nestlings hatched, and probably much less, their father had learned of their presence in the dark hollow and started to bring food to them. But his hesitancy to enter the bamboo showed plainly that he had not yet done so often. Since he had not been in the habit of entering the hollow to inspect the nest, I surmise that he was prompted to bring food by seeing his mate do so.

Even the following morning, when I watched from 5:22 until 10:00, the male flycatcher had not become a dependable provider. Although he arrived five times with insects, he ate or carried away all but one of them. To deliver this he went to the entrance five times. Thrice he left without going in; once he went part way in and made a low, purring sound; and only on his fifth visit did he disappear inside, to emerge with empty bill after, apparently, delivering the insect to a nestling.

Without their mother's care the day-old flycatchers might have starved. Although often she darted into the bamboo so rapidly that I could not see whether she carried food, she probably fed one or more nestlings each time she entered. On this assumption, she fed the brood of three 18 times in four hours, or at the rate of 1.5 times per nestling per hour. Assuming that she brooded each time she stayed in, out of sight, for more than one minute, she did so 11 times in 231 minutes (omitting nine minutes because I missed a departure). Her 11 sessions of brooding ranged from 3 to 19 minutes, totaled 97 minutes, and averaged 8.8 minutes. Her 11 absences ranged from 2 to 20 minutes, totaled 134 minutes, and averaged 12.2 minutes. She brooded for 42 per cent of the time.

During the first four hours and 20 minutes of 17 April, when the three nestlings were five days old, they were fed 16 times, at least seven times by each parent, and twice when I could not tell the food-bringer's sex. Early in the morning the male still hesitated to enter the nest. He carried away the first insect that he brought, and delivered the second only on his third approach to the entrance; but soon he was taking in food without procrastination, as the female did. Although at five days of age the nestlings apparently were fed no more frequently than when one day old, their meals were more substantial. I recognized only insects with wings still attached, including at least five skipper butterflies (*Hesperiidae*) and two small dragonflies. The female brooded five times, for intervals ranging from 6 to 14 minutes and totaling 56 minutes. She was in the nest for only 21.5 per cent of the cool, cloudy morning.

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Two days later the nestlings lay dead in the hollow bamboo. I do not know what happened to their mother. There were no shed feathers to suggest that she had been trapped in the nest by an invading predator. Both parents vanished, and I found no replacement nest.

Early in the following year I placed a number of lengths of bamboo, similar to that which held the ill-fated nest, on posts by the woodshed and in trees in the neighboring pasture. My efforts to entice a pair of Dusky-capped Flycatchers to nest accessibly once more were futile. In June I found a pair carrying insects into a hole made and abandoned by Golden-naped Woodpeckers, about 30 m up in a widely exposed dead tree, at the edge of the pasture where my lengths of bamboo rested without tenants.

In the Motagua Valley of Guatemala I found Dusky-capped Flycatchers less elusive than in the Valley of El General. While with difficulty I removed four eggs through a narrow knothole in a fencepost and measured them, a parent perched within arm's length on a leafless twig, silently watching with bright brown eyes and open, panting mouth, for the afternoon was intensely warm. A movement of mine sent her away but in a minute she returned to the same perch to watch me write in my notebook. With the exception of a Bicolored Antbird (*Gymnopithys leucaspis*), I can recall no other parent bird that looked on so intently while I described its nest and eggs. Soon I replaced the eggs so that she could return to them. Two days later the nestlings hatched, only to be destroyed by fire ants.

The nest in the broken-off stub on the scrubby hillside in the same locality contained four eggs that hatched the day after I found them. Thirteen days after hatching three nestlings, well feathered in the pattern of their parents, rested in the snug cranny. When, one by one, I painstakingly lifted them out for inspection and possibly a photograph, they snapped their broad, flat, black bills with white flanges, making loud, clacking sounds, and struggled to escape. Two slipped through my fingers and flew too well to be caught. They alighted off in the thicket, where they repeated long, plaintive whistles, similar to those of adults but weaker, which drew both parents. When the adults heard the third fledgling crying as it struggled in my hand, they darted at my head with such loudly clacking bills, such swiftness and vigor, that, despite my resolution to remain immobile and see how close they would come to me, I ducked at the crucial moment to protect my eyes. After several of these menacing darts the two parents retired a short distance to protest with long-drawn whistles that, in the circumstances, sounded more than ordinarily forlorn. I replaced the third fledgling in the hollow without expecting it to stay. Doubtless, if undisturbed, the three would have remained at least until the following day when they would have been just two weeks old.

SUMMARY

The most widely distributed species of *Myiarchus*, the Dusky-capped Flycatcher has great ecological tolerance, inhabiting semi-arid regions as

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well as rain forest, from sea level up to timberline in the tropical Andes. To a diet of insects caught in the air, plucked from foliage, or gathered on the ground it adds a few berries and arillate seeds. Although often solitary, in the Valley of El General it is found in pairs in January and occasionally in December.

In the nesting season males sing a prolonged dawn song of varied notes. A similar performance is often heard on cloudy afternoons.

Nests are built in cavities in trees or fence posts, hollow bamboo stems, and similar situations. In some localities, such as the Caribbean lowlands of northern Central America, they are often less than 2 m above the ground; but elsewhere they tend to be high, sometimes as much as 30 m.

At several nests only one bird, evidently the female, was found building. This was at unpredictable times, so that the nests might easily have escaped detection. For short periods females brought material every two or three minutes, but much of their building was more sporadic. The nest is a loose mass of the most varied materials, including seed down, soft fibers, straws, feathers, mammalian hair, and often snake skin.

Clutch size exhibits the "latitude effect." In Costa Rica and Trinidad three eggs are laid; in northern Central America and southern Mexico four; in Arizona four or five.

Only the female incubates, with the low constancy typical of small flycatchers. One female was in her nest for 51.4 per cent of 10 hours; another, for 53.1 per cent of 6.5 hours. An incubating female often sang a nest song of low, soft notes, especially when her mate was nearby. The incubation period is unknown.

Only the female broods the nestlings, but both parents feed them, chiefly with winged insects, including skipper butterflies (Hesperiidae) and small dragonflies. One male started to feed the nestlings less than 24 hours after they hatched, but at first his attendance was unreliable. Parents spiritedly defend their young.

Thirteen-day-old nestlings flew well but, if undisturbed, they would probably have remained in their nest at least one day longer.

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Myiobius barbatus

In humid forests from southeastern Mexico to eastern Peru and southeastern Brazil one of the birds most likely to attract attention is a moderately small flycatcher that flits through the lower levels, with tail fanned out and wings drooping, displaying a bright lemon-yellow rump. Above, the Sulphur-rumped Flycatcher is elsewhere dark greenish olive, with dusky wings and black tail. Below, it is largely canary yellow, suffused with cinnamon or tawny brown on the breast and sides. The male has a concealed yellow crown patch; on the female it is poorly developed or lacking. The flycatcher's

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large eyes are dark. Its short bill, surrounded by long rictal bristles, has the upper mandible heavily clouded with black to almost wholly black; the lower mandible is flesh-colored with a dusky tip. The legs and toes are blackish. From the lowland forests this flycatcher ranges upward to about 1,200 m in Costa Rica and Panama, but it appears not to have been found above 500 m in Guatemala (Land, 1970). In Honduras, however, it has been recorded up to 1,500 m (Monroe, 1968).

Restlessly active as any wood warbler, the Sulphur-rumped Flycatcher appears to subsist wholly upon insects, which it snatches from the air or plucks from foliage as it weaves airily through the higher shrubs and lower boughs of trees, in mature rain forest, taller second-growth, or along well-shaded watercourses between clearings. Never pairing, intolerant of other individuals of its own species, the Sulphur-rumped Flycatcher joins mixed flocks of small insectivorous birds that roam through the woodland. Sometimes it forages above army ants, catching insects that try to escape the hunting horde by flying. Its usual note is a low, sharp *psit*, *fit*, or *pit*, often uttered in flight. Only with extreme rarity have I heard a Sulphur-rumped Flycatcher give a more elaborate vocal performance. One individual, whose conspicuously spread, bright yellow crown patch revealed that he was a male, uttered five high, sharp notes, followed immediately by the same number of softer, warbled notes. Another, in the undergrowth of second-growth woods, sang *cheu cheu cheu cheu* in a pleasant voice. In contrast to Ochre-bellied (*Mionectes oleagineus*), which also fail to pair, Sulphur-rumped Flycatchers have not been found in singing assemblies; and their courtship has not been witnessed.

NEST

The Sulphur-rumped Flycatcher's pensile nest is attached to a slender vine, spray of climbing bamboo, or thin twig hanging in a clear space amid the forest, above a woodland path, over a stream or pool, or at the edge of a pasture. Since the nest is so conspicuous, for safety it must dangle free of surrounding vegetation that would make it readily accessible to climbing predators. The extreme range in height of 24 nests was 1 to 11 m. However, only one of these nests was above 6 m, and only one below 1.7 m. Eighteen were from 1.7 to 3.7 m up. Some could be inspected by gently drawing them down to within hand reach with a hooked stick, then permitting them to rise slowly to their original position.

All the nests that I have watched were built by a single, unaccompanied individual, undoubtedly a female. Elsewhere I have described and illustrated (1960: fig. 94; 1976: fig. 12) how she wraps strands around the end of the hanging support until she has a small, loose mass of fibrous materials. Then, working upward, she begins to spread these materials apart, making a hollow in the bottom of the mass, surrounded by a wall that is thicker on one side than on the other. Now she takes much of her material into the hollow, in addition to attaching more to the top and sides. She continues to push the mass apart, enlarging the cavity, and at the same time she

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extends the lower edge of the thicker side inward as a rim, which eventually becomes the bottom of the brood chamber.

The completed nest is a pyriform or nearly conical structure, tapering upward from the rounded bottom to the pointed apex where it is attached. It contains a rounded chamber with a sideward-facing doorway. This opening faces an enclosed space, or antechamber, screened by an apron continuous with the side walls of the chamber. To enter her nest the bird must fly straight upward into the antechamber; to examine its contents, one must feel with a finger or insert a small mirror, as it is impossible to look straight in. The fibrous materials of the nest are brownish and form a loose meshwork on the sides. The floor of the chamber is thickly lined with fine, light-colored fibers. A typical structure was about 22 cm high, not including fibers protruding at both ends; near the bottom, where it was widest, its diameter was 9 cm. Sometimes fibers and other materials are wrapped around the supporting vine or twig above the actual top of the nest, occasionally for as much as 40 cm.

These nests, like the pensile structures of many different shapes built by other American flycatchers, are formed by a process of felting or matting, or entangling and compacting fibrous materials, rather than by weaving them into a fabric, which flycatchers appear unable to do. Thus, in their mode of construction they differ greatly from the woven pouches of oropéndolas, orioles, and weavers. Since the construction of the Sulphur-rumped Flycatchers' elaborate nests is time-consuming, sometimes taking as much as three weeks, they are begun long before eggs are laid. In the Valley of El General I have known them to be started as early as the last week of January, although I have found no eggs until March.

EGGS

Each of 11 accessible nests contained two eggs or nestlings. The eggs are laid early on alternate days. At one nest the first egg was laid before 7:10 on 15 May; the second between 7:00 and 9:00 on 17 May. The eggs are white, grayish white, or light grayish pink, marked with chocolate or rufous brown, which may occur as fine speckles over the whole surface, as irregular flecks and scratches covering the egg in a most curious pattern, or as a heavier mottling. Usually the pigmentation is heaviest in a wreath around the middle or the thicker end, where it may cover most of the surface. The measurements of 10 eggs average 18.2 by 13.1 mm. Those showing the four extremes measured 19.1 by 12.7, 17.5 by 13.5, and 18.7 by 12.3 mm.

In 14 nests in the Valley of El General, 600 to 900 m above sea level, eggs were laid as follows: March, 5; April, 4; May, 3; June, 2.

INCUBATION

Only the female incubates. One slept in her nest at least four nights before she laid her first egg, and during the two additional nights before

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her second egg was laid, thereby revealing a tendency, more developed in other flycatchers such as the Sulphury Flatbill (*Tolmomyias sulphurens*), to use the breeding nest as a dormitory. However, another Sulphur-rumped Flycatcher occupied her nest at most one night before it contained an egg.

At a nest that hung above a narrow, nearly dry watercourse in tall second-growth woods, where the eggs were within a few days of hatching, I made several watches which together covered all hours of the day. Between her first departure at 5:29 and her entry for the night at 16:58, this flycatcher took 22 sessions, which ranged from 7 to 33 minutes and averaged 14.1 minutes. Her 23 recesses varied from 8 to 28 and averaged 15.6 minutes. She was in her nest for only 47.5 per cent of her active day.

Returning from an excursion this Sulphur-rumped Flycatcher alighted on a slender, horizontal twig, a few meters from her low nest and at the same height. From this perch she made a number of swift sallies to snatch insects from the air or foliage, delaying her return to her eggs. Finally, her hunger satisfied, she darted up into the nest, where she clung upright in front of the chamber, with her tail pressed against the side of the nest below her. Then, as she settled into an incubating posture, her tail rose until it became nearly horizontal, as I could see through the meshes of the apron that covered the antechamber. She always sat with her head inward and her tail projecting into this space. Without the shielding apron her yellow rump would have been conspicuous from above. Often she voiced a sharp *pit* as she shot upward into her nest. To leave she reversed the movements she had made on entering, first rising into a nearly upright position at the doorway, then darting out.

Another female watched for a morning, took seven sessions that ranged from 15 to 30 minutes and averaged 23.1 minutes. Her seven recesses ranged from 14 to 47 minutes and averaged 24.6 minutes. She incubated her eggs only 48.5 per cent of six hours. Such poor constancy is not unusual among small flycatchers, especially those with hanging nests, and is probably at least in part responsible for their unusually long incubation periods.

At four nests of the Sulphur-rumped Flycatcher the incubation period was 22 days. The closest determination was 22 days \pm 2 hours. Gross (1964) found the incubation period of the closely related Black-tailed Flycatcher (*Myiobius atricaudus*), in the warmer forests of Barro Colorado Island, to be 21 days.

NESTLINGS

The hatchlings are blind, with no trace of down on their dark skins. The lining of their mouths is yellow, as in other flycatchers. As their parent built the nest and incubated the eggs with no attendant male, so she raises her young quite alone, as I have seen at no less than six nests. She nourishes them chiefly with winged insects, including moths and some with lacy wings. Occasionally she brings a butterfly too big to be readily swallowed, but instead of knocking off the wings, as many birds do, she presents it to the nestlings

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again and again until it vanishes. To deliver food she clings upright in front of her doorway, under the protecting apron, with her tail pressed inward against the nest's bottom. Then, if she does not stay to brood, she drops out tail-first. Two nestlings six and seven days old were fed 54 times in four hours, or at the rate of 6.8 times per hour for each of them. After these same two nestlings were feathered, they received 66 meals in two hours, or at the rate of 16.5 meals per nestling per hour.

The nestlings develop slowly. The naked skin, dusky when they hatch, darkens until it is nearly black, at least dorsally. Not until they are six or seven days old do the feather rudiments begin to emerge from the downless skin. When they are about two weeks old their plumage begins to shed the horny sheaths and expand; at 16 or 17 days of age they are fairly well clothed. From an early age they lie in their nest with their heads at the back, just as their parent sits to incubate and to brood. In this orientation they can void their droppings over the opening, at least after they are somewhat grown. The fecal sacs fall to the ground and the parent does not need to remove them.

It is difficult to learn whether older nestlings are still at home, without causing their premature departure. When I looked in, two 21-day-old young darted from their nest, voicing a sharp *fit* much like that of the adults, and flew too well to be caught. They took refuge in a fringe of bushes along the river bank where their mother brought them food. Another 21-day-old nestling, raised alone, also fled from the nest when I tried to learn whether it was still present. Two other young left spontaneously when 23 days of age, and one at 24 days. In their bright new plumage, including the yellow rump, fledglings closely resemble adults but the colors of their underparts, especially the tawny of the chest, are paler.

One female slept in her nest for at least one night after her single fledgling left it, further illustrating the tendency to use the breeding nest as a dormitory.

Allowing about three weeks for building, 2 days for laying, 22 days for incubation, and 23 days for rearing the nestlings, a single nesting takes about 68 days. I do not know how long parental care continues after the young fly, but it is probably no less than two or three weeks. Accordingly, it is doubtful whether any parent produces more than a single brood in a year. One Sulphur-rumped Flycatcher was still feeding nestlings in early August, but probably she had lost, rather than raised, one or more earlier broods.

"BLACK-BREASTED MYIOBIUS"

On 26 May 1942 I discovered in the forest at Los Cusingos a typical Sulphur-rumped Flycatcher's nest, which was attended by a bird that differed from any member of this species that I had hitherto seen. The one very obvious difference was that her lower breast was crossed by a broad, blackish band, slightly interrupted in the middle. I saw no other individual of this description until 14 years later when a similarly dark-breasted bird built

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a nest only 1.7 m above ground at the woodland's edge, beside a pasture. Since this was the most conveniently situated for study of any nest of *Myiobius* that I had so far found, I devoted much attention to it, and enjoyed excellent opportunities to scrutinize its builder at the closest range of my eight-power binoculars.

Her upper plumage closely resembled that of a normal Sulphur-rumped Flycatcher. Her chin and throat were pale yellowish gray, and posterior to this, on the chest, was a prominent crescentic patch of orange-tawny, of the same shade as that of a normal individual, but much narrower. Its posterior margin abutted abruptly on a very broad zone of dull black or deep slate-color, that covered her breast, sides, and upper abdomen, and was marked by many fine, longitudinal, whitish streaks. Her remaining underparts were pale yellow, as in a normal Sulphur-rumped Flycatcher. The tawny feathers of the chest stood out beyond the dark feathers posterior to them, seeming to be fuller and thicker. By contrast, the blackish feathers appeared to be worn, or possibly matted down by wetting. Yet, in the approximately two months that I kept this bird under observation, I detected no change in the dusky ventral band.

My careful study of this nest and its attendant revealed no differences from normal Sulphur-rumped Flycatchers in behavior or development, except that the eggs were more pinkish and more heavily marked with rufous-brown than others that I had seen. Nevertheless, in view of the uncertain relationship of the dark-breasted birds, when I wrote my life history of the Sulphur-rumped Flycatcher (1960), I gave my observations on this nest under a separate heading, "The Black-breasted *Myiobius*." Wetmore (1972) surmised that the black-breasted individuals were "apparently partially melanistic."

Later observations have clarified the problem of these dark-breasted birds. In mid-June 1962 I found a normal Sulphur-rumped Flycatcher building an exceptionally late nest, during a week of drier weather after a very wet late April, May, and early June. By late July, when this female was feeding nestlings, I noticed dark streaks appearing in a band across her lower breast, which had been orange-tawny. In the following weeks, the dark color increased in this region. It was less intense in the center of the breast than toward the sides.

Ten years later, in early March, I found a typical Sulphur-rumped Flycatcher attaching a nest to a dangling spray of climbing bamboo (*Chusquea* sp.) at the edge of the pasture in front of the house. By late April, when this female was feeding a nestling, patches of pale gray were appearing at the sides of her breast. These grayish patches deepened in tone and grew inward until they coalesced, forming a broad, deep slaty or dull black band across her lower breast and upper abdomen. This dark zone had a very irregular posterior margin and was marked with fine, light streaks. It continued to spread until by the second week of May it extended broadly from the tawny chest to the middle of the abdomen. This flycatcher now closely resembled the "Black-breasted *Myiobius*" that I had earlier studied.

One nestling in this earlier nest succumbed when its nest, sodden by

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a heavy rain, broke the thin supporting strand of climbing bamboo, fell, and was tied up as close to its original site as I could attach it. As the surviving nestling became clothed with plumage I noticed dark gray feathers, just escaping from their sheaths, at the center of its breast. They were much shorter than the buffy ochraceous and pale yellow feathers that bordered them at the sides and covered them. When this progeny of a dark-breasted mother fledged it was no different from any other juvenile that I have seen.

The prominent dark pectoral band, which might cause certain Sulphur-rumped Flycatchers to be taken for a distinct species, is evidently caused by abrasion, or possibly insect damage, of feathers on the breast and sides during nest attendance, exposing darker under plumage that was always present. No other female bird that I have studied has changed so greatly in appearance while attending a nest.

SUMMARY

A solitary bird that forms no lasting pairs, the Sulphur-rumped Flycatcher flits through the lower levels of humid Tropical Zone forests, with tail fanned out and wings drooped to expose a bright yellow rump. A single individual often joins a mixed flock of insectivorous birds. It subsists upon insects snatched from the air or foliage, and apparently eats no fruit.

Its nest is a pyriform or roughly conical structure, attached by its pointed apex to a dangling vine or twig, and containing a rounded chamber entered through an antechamber that opens downward. Its construction, by an unattended female, may take as much as three weeks. In the Valley of El General building sometimes begins in late January, although eggs have not been found before March. Twenty-four nests hung from 1 to 11 m above ground or water, but most were 1.7 to 3.7 m up.

The two eggs, laid in the morning of alternate days, are incubated by the female alone. She sits with very low constancy, often slightly less than 50 per cent, which may account for the long incubation period of 22 days.

The young hatch with dark skin devoid of down. They are nourished with insects, mostly winged, by their mother alone, at rates up to 16.5 times per hour for each of them. They rest with heads toward the back of the nest, the orientation of the incubating or brooding parent and, when older, defecate over the doorsill so that the droppings fall through the antechamber to the ground. Their development is slow. The full nestling period is 23 or 24 days; but, if disturbed, the young jump out and fly well a few days earlier.

The female sometimes uses her well-enclosed nest as a dormitory, sleeping in it for several nights before she lays her first egg, and again after the young have left.

While nesting some females develop a broad, dark-slaty or blackish band across the breast, which makes them appear to be a different species. This transformation, unique in my experience with nesting birds, appears to result from plumage wear or insect damage.

GREENISH ELAENIA

GREENISH ELAENIA

Myiopagis viridicata

A quiet, inconspicuous flycatcher about 13 cm long, the Greenish Elaenia readily passes undetected, and, if noticed, is easily confused with other small, plainly colored members of its huge family. Its upper plumage is largely olive-green, more grayish on the crown, in the center of which is a usually concealed patch of bright yellow. A whitish line extends from the lores to above each eye, which is surrounded by an indistinct light ring. The remiges and their coverts have contrasting greenish or yellowish margins but lack well-defined wing bars. The light gray of the throat and breast blends into yellow on the more posterior underparts. The short, straight, narrow bill, feet, and toes are blackish, and the eyes are brown. The female closely resembles the male but has less yellow on the crown. A Greenish Elaenia watched carefully and continuously will often spread its crown feathers enough to disclose more or less of the underlying yellow, which distinguishes it from the other small greenish or grayish flycatchers likely to be confused with it, at least north of Panama. In central and eastern Panama the very similar Forest Elaenia (*M. gaimardii*) is distinguished by its prominent wing bars.

The species ranges from the Mexican states of Nayarit and Tamaulipas through Central and South America to western Ecuador, Venezuela, and northern Argentina. A bird of the Tropical Zone, the Greenish Elaenia extends upward to 900 m in Mexico (Miller *et al.*, 1957), 1,200 m in Guatemala (Land, 1970), 900 m in Honduras (Monroe, 1968), 1,500 m in western Panama (Wetmore, 1972), and 1,000 m in Venezuela (de Schauensee and Phelps, 1978). In Costa Rica I have found it fairly abundant around 1,200 m and sparingly present 300 m higher.

A species of such wide geographical range is usually somewhat variable in its choice of habitats. I have most often found it in groves of medium-sized trees and light second-growth woods, especially near streams; and this has been the experience of others, including Carriker (1910) and Ridgely (1976). I have also seen these birds in the more open parts of rain forest, especially near its edge; and Wetmore (1972) found them "mainly in the tops of undergrowth in the forests, where they moved quietly, usually alone, occasionally in company with small groups of other birds. In Chiriquí and in the Province of Los Santos in the Azuero Peninsula they were mainly in heavier stands of forest." At the other extreme, they inhabit sparsely wooded savanna in the Orinoco region (Cherrie, 1916) and thorn thickets in Morelos, Mexico (Rowley, 1962). I have nearly always found Greenish Elaenias alone, except when they are nesting.

FOOD

Greenish Elaenias forage mainly within the crowns of trees rather than in the open. They make short darts and, without alighting, pluck small

GREENISH ELAENIA

creatures from leaves, bark, or inflorescences. Among the vegetable foods that I have seen them take are arillate seeds of the vine *Davilla Kunthii* (Dilleniaceae) and of the trees *Casearia sylvestris* (Flacourtiaceae) and *Zanthoxylum procerum* (Rutaceae), and the small berries of the shrub *Miconia minutiflora* (Melastomaceae). Wetmore (1972) also occasionally saw them eat drupes of shrubs and trees.

VOICE

The call of the Greenish Elaenia is a thin, sibilant note or low, harsh whistle, which at times might be mistaken for the Sulphury Flatbill's (*Tolmomyias sulphureus*) call. At dawn these little flycatchers continue for many minutes to repeat a twilight song in which, over the years, I have noticed considerable differences in phrasing, although the performance is always weak and droll rather than loud and brilliant. One elaenia sang *peer-weer peer-weer peer-weer* . . . in a small, unobtrusive, almost tremulous voice. Another, in the same grove of guava trees (*Psidium Guajava*) between two streams, repeated *peer weedyum peer weedyum* interminably. Years later, in another part of the Valley of El General, an elaenia sang at dawn *peer pee peer pee peer pee* many times over, in a high, thin voice. Another elaenia's twilight song sounded more like a lisping *see-e seer seer see-e*. Often the plain little bird proclaims his presence at the very top of a tall tree with an open crown, where he flits from branch to branch as he sings. I heard these dawn songs in April 1939 and May 1969, when such performances are expected of flycatchers, and, perplexingly, in August 1967 and 1968 and early September 1963, when few birds of any kind sang at daybreak.

Long after sunrise in early May a Greenish Elaenia sang for many minutes *we cher cher we we cher cher we cher cher* in a small, high-pitched voice—a lazy, comfortable performance that suggested a placid nature.

NESTING

Rowley (1962), who in Morelos, Mexico, discovered nests of the Greenish Elaenia from 4.5 to 7.8 m up in thorn thickets, confessed that "finding a nest was one of the most tedious and frustrating experiences I have ever had . . . My experience with these four nests convinces me that it is nearly impossible to find a nest of the Yellow-crowned [or Greenish] Elaenia unless the female leads one to it."

My own experience was similar. This elaenia is one of the less abundant flycatchers at Los Cusingos, but not so rare that it should not now and then be found nesting. Nevertheless, year after year its nest eluded me until, on the brilliant morning of 11 May 1979 I happened to notice a female just starting to build. Her site was about 6 m up at the top of a tree of *Oliganthes discolor* (Compositae) growing at the edge of an open grove of these trees, on a steep, sterile hillside that had formerly been pasture. The horizontal fork of the thin branch to which she was attaching

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material was shaded by large leaves above but quite exposed on the sides and below. As far as I saw in four hours of watching, only one bird built. When I discovered the nest a few bits of fine material had been strung between the arms of the fork. In the hour from 7:35 to 8:35 the builder brought material 18 times, and six times more in the next half-hour. At first she brought cobweb on most of her visits and carefully spread it over the supporting arms. As building advanced she increasingly brought such other materials as slender rachises of small compound leaves, pieces of tendrils, or fibrous roots—always small, fine pieces. All this came from a distance, apparently the neighboring woodland. Rarely the builder emitted a low, sibilant note. Sometimes when she bent down her head to arrange the nest I glimpsed the usually hidden yellow patch on her crown.

Two days later, from 6:50 to 8:50 on 13 May, the elaenia came to her nest only 11 times, bringing more cobweb and other materials that were always slender and stiff, including rachises and pieces of tendrils. Rarely her mate appeared in a neighboring tree, or followed her as she flew off for more materials, but he did not come near the nest. After five days of increasingly leisurely work, the slight structure appeared to be finished. It was a shallow cup or bowl, so thin that, when eggs were laid, they were plainly visible through the many meshes of the bottom, which was fortunate, as I could not otherwise have seen them on a long branch far too thin to support a climber. This nest closely resembled that illustrated by Rowley (1962: fig. 1).

At 7:15 on 18 May an egg was present, and another was laid two days later. At daybreak on 23 May I climbed the hill to the nest, intending to watch it all morning. When the light increased I saw, to my dismay, that it was empty.

After much searching for a replacement, on 4 June I found the female finishing a new nest, about 10 m up in another *Oliganthes* tree and 18 m down the slope from the site of the first nest, which meanwhile had wholly vanished. The situation of this new nest was very similar to that of the first. Building continued on the following day; and the first egg of the replacement set was laid on 6 June, 14 or 15 days after the loss of the first set. During the two nights which intervened before the second egg was laid the female evidently slept on the nest, where she was present at nightfall; but I did not find her incubating during the intervening days.

Each of Rowley's four nests in Mexico held two eggs or young. Those of one set measured 18 by 13 and 17 by 12.5 mm and were handsomely marked with heavy lilac and chocolate-brown streaks and blotches over most of the (white?) surface. In these Mexican nests eggs were laid from May to early July.

I watched the second nest from 5:12 to 12:07 on the morning of 10 June, and from 12:00 to 18:12 the following afternoon. Although I could not with certainty distinguish the sexes, I saw no changeover, nor anything to suggest that the male shared incubation. The female's 22 sessions ranged from 7 to 49 minutes and averaged 19.4 minutes. The longest came at

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the day's end; the next longest, 28 minutes, early in the morning. An equal number of recesses ranged from 4 to 37 minutes and averaged 12.7 minutes. The female was on the nest for 60.5 per cent of her active day of nearly 12 hours (5:31 to 17:10), which is about normal constancy for a small flycatcher. Thrice she returned to incubate bearing a fine piece of material that she added to the nest.

Little more than the abdomen of the incubating female fitted into the slight, shallow nest. Her head and neck, wings and back, long tail and undertail coverts all rose above its rim or projected beyond it. The safety of this small, rather exposed nest appeared to depend largely upon the incubating bird's failure to attract attention because she sat motionless. Nevertheless, she constantly turned her head from side to side, looking around. At intervals she preened, or rose up to poke down into the nest. When spots of sunshine fell upon her through gaps in the canopy above, she panted. And she came and went frequently, instead of sitting motionless for long intervals in her inconspicuous nest, as manakins and Rufous Pihas (*Lipaugus unirufus*) do. However, she was silent.

The male kept no consistent guard, but he often came to the nest tree and chased, or tried to chase, intruding birds. A Golden-naped Woodpecker (*Melanerpes chrysarchus*) retreated when threatened, but a Black-striped Sparrow (*Arremonops conirostris*) refused to budge. When a Squirrel Cuckoo (*Piaya cayana*) flew into the treetop, the female jumped from her eggs to help her mate drive it away; and both darted at a Vermilion-crowned Flycatcher (*Myiozetetes similis*) until it departed. Once or twice the male appeared to pluck something, probably an insect, from the outside of the nest. All this occurred during the forenoon. With one possible exception, the male remained out of sight all afternoon.

By 13 June the eggs had vanished from this second nest, leaving the structure intact. Possibly one of the Swallow-tailed Kites (*Elanoides forficatus*) that at intervals soared overhead had detected it through gaps in the canopy of foliage above it. Although these graceful birds subsist largely upon flying insects which they seize with their feet while they circle high in the air, they plunder nests that they can reach while hovering.

I searched for another replacement nest, but found none. In the following year, however, the female built again in the same small clump of *Oliganthes* trees where she had twice failed to hatch her eggs. On 16 May 1980 I found her finishing a nest about 6 m up in the triangular space between two diverging twigs and a thin vine that crossed them. Neatly fitting into this space, the nest was attached only by its rim, with no support below. Through the thin bottom I could see the two eggs that were laid on 22 and 24 May, the second between 7:35 and 14:00.

On 2 June, a morning alternately sunny and lightly clouded, I watched the female incubate from daybreak until noon. Her 16 sessions ranged from 7 to 30 minutes and averaged 9.7 minutes; her 16 recesses, from 3 to 20 minutes and averaged 9.7 minutes. She sat with a constancy of 60.8 per cent, which is surprisingly close to her record on the forenoon

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of 10 June of the preceding year, when she incubated for 61.6 per cent of the time, although then both her sessions and recesses averaged about two minutes longer. Especially toward the end of the morning of 2 June, the elaenia sat restlessly, preening in the nest, turning around, frequently rising up or standing on the rim to poke down into the cup, as though vermin bothered her. She did not bring anything to the nest, as on the previous morning. Early in the day the male often came to the nest tree, but after mid-morning I failed to see him. Three days later these eggs also vanished.

SUMMARY

The Greenish Elaenia is most often found in scattered trees, open groves, and light woods, but it also enters rain forest. When not nesting it is usually solitary.

Its food consists largely of insects plucked from foliage, bark, or inflorescences on short darts within the crowns of trees. It also eats berries and arillate seeds.

Its calls include thin, sibilant notes and low, harsh whistles. At daybreak it sings a prolonged dawn song in a weak voice. These songs have been heard in April, May, August, and September.

Only the female was found building. Three nests, situated 6 and 10 m up in exposed treetops, were open cups so thin that the eggs were visible through the meshes of the bottom. These Costa Rican nests closely resembled those found in Mexico.

In May two eggs were laid with an interval of two days. Fourteen or 15 days after the loss of these eggs the female laid another set of two in a neighboring nest.

Only the female incubated, with a constancy of 60.5 per cent. During the forenoon her mate was often present and drove intruding birds from the nest tree, but in the afternoon he remained away.

After the loss of the second set of eggs, no other nest was found until the following year, when another set of eggs was laid in May and lost.

SOUTHERN BEARDLESS FLYCATCHER

Camptostoma obsoletum

A tiny, small-billed, inconspicuous flycatcher, the Southern Beardless is only 9 cm long. The sexes are alike. Above they are plain greenish olive, slightly darker on the crown, which lacks a concealed bright patch. The dark gray tail feathers have narrow light tips. Two white or yellowish bars and narrow pale edgings on the remiges mark the dusky wings. An inconspicuous, pale gray streak extends from the lores to above each eye. The cheeks are gray; chin and throat very pale gray; and the remaining underparts pale yellow. The eyes are brown. The short, straight, narrow

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bill, legs, and toes are blackish. The crown feathers are often partly erected into a low, loose crest, giving a characteristic aspect to this little bird of undistinguished plumage. Voice and the habit of wagging the short tail up and down also help identify it.

The species ranges along the Pacific slope of Costa Rica southward from the Tempisque Valley in Guanacaste and through Panama and South America to Bolivia, northern Argentina, and the Guianas. In Costa Rica I have not noticed it above 750 m; but in Venezuela it has been reported as high as 1,100 m (Phelps and Phelps, 1963), and in southern Brasil at 900 m (Mitchell, 1957). Singly or in pairs, never flocking, it inhabits light, open woodland, scrubby vegetation, savannas with scattered trees, shady plantations and gardens. Although I have not noticed this flycatcher in closed forest, Wetmore (1972) found it in heavy forest, often in high tree crowns, in humid regions on the Caribbean side of Panama.

FOOD

As has been noticed by some authors, in their manner of foraging these tiny flycatchers resemble wood warblers or vireos. They hop and flit through the branches of trees and shrubs, often high but sometimes low, plucking minute creatures from leaves, twigs, or fruits. Occasionally they gather something from a solid surface while hovering on wing, but they rarely catch flying insects, an omission that is probably related to the absence of more than rudimentary rictal bristles indicated by their name "Beardless." While foraging the little flycatcher tilts its short tail upward and wags it up and down, occasionally raises its crest, and from time to time calls. Its diet includes coccids, ants, spiders, and small berries (Haverschmidt, 1968).

VOICE

The thin, high-pitched, not unmusical notes of the Southern Beardless Flycatcher are distinctive, often revealing its presence in the crowns of leafy trees where it forages unseen. Sometimes as many as ten notes are delivered in falling cadence. In the Valley of El General it is consistently the first flycatcher to deliver its dawn song and to nest. With the first promise of the approaching dry season the male mounts to a high, exposed twig, often at the very top of a tall, dying or dead tree, to repeat over and over, in the dim early light, a phrase that sounds like *te be be be*, or at times *te be be be be*. Although the notes are now slightly deeper and fuller than the daytime calls, they have the same penetrating quality that makes them unmistakably his. While proclaiming his presence on the high treetop, he slightly erects his crown feathers and turns his head restlessly from side to side. At first he tends to stay on the same perch but, as the performance continues in the growing daylight, he may fly from tree to tree, and he interjects more call notes into his dawn song, which may last for nearly half an hour. One morning, when the performance was especially prolonged,

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I counted 21 phrases per minute at the outset, 17 somewhat later, but only six when he was tiring toward the end.

After a few days of drier weather I heard dawn singing at the exceptionally early date of 11 November 1962. Often it begins in the first ten days of January and continues until March or early April. A beardless flycatcher that sang at dawn on 24 July 1960 was not heard on subsequent mornings. Evidently some exciting event had stimulated this outburst in the midst of the rainy season, when beardless flycatchers are mostly silent.

NEST BUILDING

In the Valley of El General a marked decline in the heavy rainfall of the second half of the year evidently stimulates Southern Beardless Flycatchers to sing at dawn and to nest. In 1969, after a few dry days following weeks of torrential rains, a nest was begun on 12 December. I have two other records of building in December, when scarcely any other passerine birds are singing or nesting.

For its nearly globular nest with a side entrance, this flycatcher prefers a site that gives support all around. Of the six nests that I have seen, two were in richly branched panicles high in trees: one of these was amid the white flowers of the arboreal composite *Oliganthes discolor*, the other among the tiny, pale red, rayed achenes of the burío (*Heliocarpus excelsior*). Two nests were embedded in dense masses of the brown liverwort *Frullania* and other small epiphytes that draped below long, ascending, nearly leafless branches of the calabash tree (*Crescentia Cujete*). Another nest was built in a cluster of the dry, prickly pods, like small chestnut burrs, of an annatto tree (*Bixa Orellana*). The sixth nest was enclosed in the folds of a large, palmately lobed, fallen leaf of a cecropia tree that had lodged on a lower branch, where it hung with its shriveled blade on one side and its long petiole on the other. Set between the curled lobes of the brown, dry leaf, this nest was excellently concealed. In height these six nests ranged from 5 to about 30 m, the highest being at the top of a tall burío tree.

On the arid Santa Elena peninsula of southwestern Ecuador, Marchant (1960) found 20 nests suspended among petioles or thin twigs of a variety of trees and shrubs, 1 to 4 m up. One was on a dead branch on a heap of sticks. Each of 12 of these 20 nests was within 1 m of a wasps' nest, usually one that was active. None of my Costa Rican nests of beardless flycatchers was near a wasps' nest; the sites that provide the concealment and support that these birds prefer here are not always close to vespiaries. In Surinam Haverschmidt (1954) discovered a nest attached to the bottom of a pensile, retort-shaped nest of *Tolmomyias* (probably the Yellow-breasted Flatbill), in exactly the same manner as a nest of a Paltry Tyranniscus (*Tyranniscus vilissimus*) that I found fastened beneath a Sulphury Flatbill's (*Tolmomyias sulphurens*) similar nest in Costa Rica (Skutch 1960: fig. 78). The tyranniscus also places its globular nests in curled dead cecropia leaves, amid dry annatto pods, and in moss or liverworts on branches; these two diminutive flycatchers build similar nests in a similar range of sites.

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On the morning of 12 December 1969, after several rainless days, with much shrill calling, a Southern Beardless Flycatcher started a nest amid brown liverworts beneath a branch of a calabash tree in view of my study window. Her site was 7.5 m above the edge of a high, steep bank and very exposed. On ensuing days she brought material to this nest as follows:

13 December, 6:40 to 8:40, 60 times in 2 hours
13 December, 9:00 to 10:00, 16 times in 1 hour
14 December, 6:50 to 9:50, 67 times in 3 hours
16 December, 7:30 to 8:30, 5 times in 1 hour
19 December, 7:10 to 10:10, 31 times in 3 hours
20 December, 9:10 to 10:10, 2 times in 1 hour
22 December, 7:20 to 9:20, 3 times in 2 hours

Building continued for 11 days, but was most active during the first week. Another individual built for at least nine days, after which she abandoned her structure.

Although I could not distinguish the sexes of these pairs by appearance or voice, my failure ever to see both partners simultaneously engaged in building convinced me that the female receives no help—a conclusion earlier reached by Haverschmidt from observations in Surinam. The first female's method of working was peculiar. Some of her materials came from beyond view. After adding a contribution that she had brought from afar, she might pluck brown liverworts or other things from branches around the nest and take these inside in rapid succession. On each of two visits she did this a dozen times, once 15 times, and on many other visits she stayed to add a smaller number of contributions from nearby sources. Then she would fly away, often crossing the open pasture at the level of the treetops, to disappear in the woods beyond the stream, whence after a while she emerged with more material. All these contributions were tucked into the space between the liverworts dangling below the branch, where the nest was taking shape. While working she called much, even with laden bill.

Rarely the male followed his mate to the nest tree, where he might perch for many minutes, idle or preening, while she toiled. Sometimes he preceded her to the nest and clung there to examine it briefly. I never detected any nest material in his bill.

While the first female was building, the unseasonably dry weather ended with heavy showers, and the sodden nest fell soon after it was finished. The ovoid structure was 13 cm high, 8 cm from front to back, and 6 cm wide. A round doorway in the side, 3 cm in diameter, gave access to a cozy chamber about 5 cm high by 4 cm wide. The nest was composed of dark brown, dry liverworts; spiny, curling, slender secondary rachises of the liana *Mimosa myriadena*; cobweb and cocoon cases. It was softly lined, especially on the bottom, with long, whitish seed down. The nest among the annatto pods was slighter, about 8 cm high by 6 cm wide, with a doorway 4 cm in diameter. In addition to many rachises of the climbing mimosa in the outer layers, it contained many shreds and large fragments of whitish

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or light gray papery material, probably from wasps' nests or egg cases of insects. The lining of balsa down was thin on the bottom and sides but thicker at the top.

A third nest was thin and flimsy, the builder evidently having depended upon the liverworts in which it was embedded to give it firmness and protection. In addition to the usual mimosa rachises, it contained green and brown liverworts and mosses, a few foliaceous lichens, many flocculent tufts of cocoon silk ranging from white to tawny in color, and some empty egg cases of spiders. The lining, again thicker on the ceiling than on the floor of the chamber, consisted of wefts of tawny seed down. The structure was a curious patchwork of materials and colors.

EGGS

In the earliest nest eggs must have been laid in mid-December, for the parents were feeding nestlings by 5 January. In the latest nest the second egg was laid between 9:25 and 13:00 on 8 February 1950. The eggs in this nest were abandoned, possibly because of the lateness (for this species) of the season, although most other small birds had not yet started to build.

The nest in the annatto was the only one that I could examine *in situ*. The two eggs were white without gloss, with fine, pale cinnamon spots in a wreath and a few scattered over the remaining surface. The spots on one were faint. The eggs measured 15.1 by 12.3 and 15.1 by 11.9 mm.

In southwestern Ecuador, Marchant examined seven sets of two eggs and two sets of three. Eggs are laid on alternate days. In Surinam, Haverschmidt found one apparently complete clutch of a single egg, and two sets of two eggs. He described them as creamy white, with a number of lilac and reddish brown spots, especially on the larger end. He gave measurements of 16.4 by 12.3, 16.2 by 12.8, 16.6 by 12.5, and 16.7 by 12.3 mm. A fresh egg weighed 1.35 grams.

In Surinam eggs were found in September, October, and December, in both the long dry season and the short rainy season. In Trinidad breeding was recorded in April, July, October, and November, apparently one nest in each month (French, 1973). In contrast to the situation in rainy southern Costa Rica, where beardless flycatchers avoid nesting in the long wet season, in arid southwestern Ecuador most nests were started after important rain from February to June, but three were known to have begun two to five weeks before any rain.

INCUBATION AND CARE OF YOUNG

I have been unable to make a careful study of incubation, as the low nest with eggs was abandoned prematurely. During a watch of 200 minutes, when attentiveness at this nest was waning, I saw no changeover. The incubating bird, evidently the female, sat in the nest either sideways or facing outward, and while there she called in her high, thin voice, answering the notes of her mate. Failure to witness a changeover also led Haverschmidt to infer that only one parent, probably the female, incubated. In Ecuador,

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Marchant found the incubation period to be approximately 15 days. His nestlings hatched with orange skin and yellowish down. The mouth lining of older nestlings that I saw was bright orange-yellow.

At two nests I have seen both parents bring food to the nestlings, although apparently only one parent brooded. One of these nests was situated 7 m up, at the top of a calabash tree. The parent arriving with food first appeared on leafless twigs at the top of taller guava and orange trees standing nearby. Here it flagged its tail up and down, turned its head from side to side, and called repeatedly while it descended by stages to the nest. Sometimes it added to the load of small insects already in its bill and mouth by picking others from the dead twigs where it paused. It fed the nestlings while standing in the doorway, tail outward, then rose higher into the trees before flying off to neighboring second-growth woods.

Marchant found the nestling period of one brood to be 16 days 18-1/2 hours \pm 7 hours. Seven of his nests were known to have failed and five to have produced fledglings. A snake took newly laid eggs from a nest only 80 cm from a small wasps' nest, on which the flycatchers apparently depended for protection.

SUMMARY

In the Valley of El General in Costa Rica, the Southern Beardless Flycatcher inhabits light, open woodland and clearings with scattered trees. Flitting, warblerlike, through the crowns of trees, it plucks tiny insects from foliage, bark, and fruits.

Its notes are high and thin. Perching on a lofty treetop, the male delivers a prolonged dawn song in a weak but shrill voice. He starts his crepuscular singing earlier in the year than any other flycatcher of the valley, often beginning in the first ten days of January, rarely in early November, and not falling silent until March or early April, when other flycatchers are in full song.

Nesting also begins exceptionally early, sometimes in December, as the rains decrease. It continues through the drier month of January and sometimes into February.

In El General, the cozy closed nest, with a round doorway in the side, is set in a richly branched inflorescence; amid liverworts and other small epiphytes draped below a slender branch; between prickly seed pods; or in a big, curled dead leaf. Six Costa Rican nests ranged from 5 to 30 m feet above the ground, but in South America much lower sites are often chosen. Only the female was seen building, sometimes bringing material as often as 30 times per hour. One nest was finished in 11 days.

The single accessible Costa Rican nest contained two white eggs with fine, pale cinnamon spots. In South America a clutch of two also appears to be the usual number, although clutches of one and three have been reported. Apparently only the female incubates. An incubation period of about 15 days was reported from Ecuador. Both parents feed the young with small insects during a nestling period of 16 or 17 days.

Family HIRUNDINIDAE
ROUGH-WINGED SWALLOW

Stelgidopteryx ruficollis

My earlier observations on Rough-winged Swallows (Skutch, 1960) were made chiefly on several pairs that nested in burrows that kingfishers and motmots had dug in low, sandy banks of the Río Morjá, a tributary of the Río Motagua in the Caribbean lowlands of Guatemala. Here I followed incubation and raising the young, and watched the latter fly from their burrows, closely followed by several adults. But neither I nor Lunk (1962), who in Michigan made a far more thorough study of the Rough-wings' breeding biology, knew much about the behavior of the young swallows after they left the nest. Since then, I have enjoyed opportunities to follow their activities after fledging, and I have also learned more about pair formation than I was earlier able to report.

PAIR FORMATION

Here in the Valley of El General, where Rough-wings of a light-rumped southern race (*uropygialis*) are resident throughout the year, I long ago noticed that they sometimes pair, and attempt to defend a territory, as early as November or December, although they will not nest until the following April. More recently, I have found evidence of pairing much earlier than this, and indications that the pair bond may persist throughout the year.

Beginning in September 1974 a pair could be found morning after morning on the topmost bare twigs of a big, dying guava tree in front of our house. Usually they perched from 30 cm to a meter apart, but sometimes hardly more than their own length. At intervals they left their high lookout to circle over the pasture in wide, irregular curves, after which they returned to the same dead twigs. One or both might be in the tree, or the air, at the same time. Often other Rough-wings circulated with them—the resident pair made no effort to defend this air space as their territory—and rarely a third Rough-wing rested in the same spreading treetop, away from the other two. This pair was present here only in the sunny mornings; in the rainy afternoons they went elsewhere. In early December one of these Rough-wings vanished and a single swallow spent much time in the guava tree.

In September of the following year, 1975, I found a lone Rough-wing perching, morning after morning, at the top of the same guava tree. By mid-October it had acquired a mate, that rested on the topmost leafless twigs with it, as in the preceding year. Thrice in one morning I saw one of them chase away a third swallow that tried to join them in the treetop. In November the pair spent less time there, but occasionally I found the two together, in the same tree, until mid-December, and they were still intolerant of intruding Roughwings.

ROUGH-WINGED SWALLOW

The swallows that rested in the guava tree in front of our house were evidently the same that nested, year after year, in an old burrow that Blue-diademed Motmots (*Momotus momota*) had dug in the roadside bank behind the house. In 1977 they raised three fledglings here and fed them in the guava tree that had so long been their watch tower. After the young swallows became independent and vanished in late June, the parents continued to rest in this tree, which was now completely dead, until it fell during the night of 17–18 August. After this they perched on the topmost leafless twigs of a tall tree of *Dipterodendron elegans* that grew nearby. Here I frequently found the two together on many mornings until the following February, although they were not present every day.

Usually they arrived around seven o'clock, as the sun rose above the fringe of trees along the neighboring river, sometimes coming together, on other mornings a few minutes apart. On 11 August one came alone. When the other did not appear after a few minutes, it went off. I saw neither during the remainder of the day. However, on other days one remained alone through much of the morning. Now the pair permitted one or more Rough-wings, once as many as six, to rest in the treetop with them, with no display of antagonism. After February 1978 the swallows were not found in the *Dipterodendron* tree but on dead twigs of a lower tree behind the house, near the burrow where they nested. Although these swallows could not be recognized individually (bands would have been difficult to detect on these short-legged birds) my observations led me to conclude that the pair remained intact from one breeding season to the next.

NESTING

From 1973 to 1977 (possibly excluding 1975) a pair of Rough-wings, evidently the same that rested in the treetops in front of the house, nested in the old motmots' burrow in a high clay cut-bank above the roadway close behind it. Each of the four shallow nests of grass and dead leaves was placed, not at the inner end of the long, curving burrow, but so far forward that at least part of it was visible from the front, just as I had earlier found in the burrows along the Río Morjá.

In 1978 the pair, that had evidently remained together since the preceding breeding season, were preparing to occupy this burrow again when other Rough-wings interfered. Soon after 10:00 on 26 March I noticed two or three pairs contending for it. They flew around and around, chasing each other in wide, irregular circles, now high, now low. If one touched another, the contact was momentary. From time to time one perched, or two rested close together; but repose was brief, for soon another flew at the resting bird and made it take wing. Occasionally one alighted briefly in the burrow's mouth. With four, five, or six contestants circulating swiftly, I could not distinguish the defenders from the invaders. While pursuing each other the swallows twittered softly, and made harsh, buzzing or grating sounds that I heard only when they passed close by me.

ROUGH-WINGED SWALLOW

This contest, involving two or more pairs, continued for seven hours, or until at least 17:00. Toward the end the swallows flew less and rested more. By evening each of the contestants must have flown many miles, all within the same restricted air space. Apparently, none was hurt; it was a test of endurance.

On the following days the struggle was resumed; but I did not see it continue so long. By 5 April a little material had been carried into the burrow, where a nest slowly took shape. When I inspected the nest on 11 April three swallows flew around, protesting with harsh, buzzing notes. Then all three rested amicably close together on bare twigs at the top of a neighboring tree. On the following afternoon I found a swallow lying dead in the motmots' burrow, tail outward. Behind the corpse I glimpsed a black head with two forwardly directed eyes shining in my flashlight's beam, apparently those of a spider. I was unable to see much of this creature, which retreated deeper into the tunnel when I removed the swallow. The dead bird's serrated outer primaries indicated that it was a male. Could the sting of the unidentified arthropod have killed him?

While I extracted the corpse from the burrow, two other swallows circled in front of it. Later they perched close together at the top of a nearby dead tree, where they were joined by other Rough-wings. On other occasions three Rough-wings have complained when I approached an occupied burrow, although no second pair was nesting nearby. Lunk (1962) recorded that "Extra birds keep appearing at nesting sites, from the time the site is first examined until the young are leaving the nest. Often their presence arouses no evident animosity, and I can only interpret the behavior, in a great many cases, as a sort of casual visiting."

While the two or three pairs were contending for possession of the motmots' burrow, I made, several meters away in the same bank, a straight burrow about 60 cm long, hoping to have two families nesting close together. No nest material was taken into this new burrow until after the swallow died in the motmots' burrow and I blocked its entrance to prevent another tragedy. Then a nest was built in my burrow, eggs laid and hatched, and young reared almost to the point of flight, when they were taken by some predator. In the following year, 1979, a pair nested in one of the short burrows that I had made, but lost their nestlings. After an interval of 19 days, during which a nest was slowly built in a neighboring burrow made by me, the first egg of a replacement set was laid.

Farther along our entrance road a pair of swallows nested in 1977 in a burrow, 60 cm long, that had apparently been dug by Buff-throated Automoluses (*Automolus ochrolaemus*) in a low bank beneath a jacaranda tree. In five of the eight nests along this roadway eggs were laid in April; in two they were laid in early May; and in the replacement nest they were laid in the first days of June. In other parts of Central America I have found Rough-wings laying chiefly in April, with a few belated sets appearing in May. Five of the nests along the roadway contained four eggs, and two

ROUGH-WINGED SWALLOW

had five eggs. Elsewhere in Central America five-egg sets are somewhat more frequent than those of four. Although mostly laid on consecutive days, sometimes those of the same set are laid at both one-day and two-day intervals. The immaculate white eggs of one set measured 19.1 by 13.1, 19.1 by 13.1, 19.4 by 13.1, and 19.8 by 13.5 mm. Near Pirapira, in the State of Carabobo, Venezuela, at an altitude of about 400 m, I found on 10 May 1966 a set of four eggs, in a burrow 45 cm long, near the top of a high cut-bank along a road.

Neither Lunk nor I found evidence that the male Rough-wing helps his mate to incubate. Although in other members of the family, including the Barn Swallow (*Hirundo rustica*), the Blue-and-White Swallow (*Pygochelidon cyanoleuca*), and the Wire-tailed Swallow (*Hirundo smithii*) of Africa, both parents sleep in the nest space, I have never found more than one adult Rough-wing passing the night in a burrow. The female may begin to sleep on the nest before an egg appears and continue throughout the period of laying. After a painstaking study of the Rough-wing's incubation period in Michigan, Lunk (1962) wrote: "An incubation period of 16 days seems as precise a one as can be determined from the information at hand." At a nest in a burrow that I made, the last of five nestlings hatched 16 days after the last of the five eggs was laid. At a Guatemalan nest where two of five eggs failed to hatch, the incubation period was at least 16 days, and at a recent nest where only two of four eggs hatched it was at least 17 days. At an earlier Costa Rican nest where all of five eggs hatched, the last did so 18 days after the set was complete. Probably incubation took so long at two of these nests because they were in burrows wet and cold from frequent rains.

Although male Rough-wings regularly feed nestlings, they may begin tardily. At a nest that I watched carefully, I saw nothing to suggest that both parents brought food during the nestlings' first four days, after which some disaster befell them. At another nest five hours of watching on the nestlings' second and third days failed to convince me that their father was attending them. Lunk (1962) wrote: "In some instances the male begins making trips to the nest (and presumably carrying food) very shortly after the young have hatched; in others it may be at least three days before he takes any part in feeding. In any event, the male's solicitude increases, until by the time the young are a few days old both parents are making trips with about equal frequency."

At one Costa Rican nest the nestlings were not brooded by night after their first week. At another nocturnal brooding continued until they were nine days old, after which they vanished. In Michigan Rough-wing nestlings were brooded at night only until seven or eight days old. Early cessation of brooding is widespread among burrow-nesting birds. Not only do the young need less prolonged brooding than those in open nests exposed to rain and nocturnal radiation, but the brooding parent is in greater danger. A predator approaching a nest in a tree or shrub might, by shaking it,

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arouse the parent in time to save itself; but one entering the mouth of a burrow could block the parent's escape and capture it along with the young.

Two of the broods raised in the motmots' burrow left at ages of 18 and 19 days. They departed two or three days earlier than the Rough-wings reared beside the Río Morjá in Guatemala, possibly because the burrows of the Guatemalan swallows faced a wide stream, whereas those in the roadside bank had trees and shrubbery close in front. Nevertheless, even at 18 days of age Rough-wings fly competently. In Michigan most of Lunk's Rough-wings abandoned their nests at ages of 18 to 21 days. Although three of his young swallows that had left the nest before their siblings rejoined them in it, this was unusual behavior. The majority of his Rough-wings did not return to roost in their burrows after their first flights, and I have never known one to do so. After a brood has flown the burrow is deserted by both adults and juveniles.

I have not known Rough-wings to attempt a second brood, and even replacement layings appear to be rare in Central America. In two instances, when nestlings were lost from my roadside burrows on 29 May and 8 June, respectively, the parents did not renest nearby. But when nestlings were lost on 14 May their mother started to lay in a nearby burrow on 2 June. When these eggs contained half-formed embryos, they were abandoned, for no apparent reason except the waning of parental zeal. A possible renesting occurred along the Río Morjá in 1932. A female that was incubating five eggs deserted them after I caught and marked her for identification. Three weeks later, on 18 May, the nest and its eggs had been covered by a newly built nest in which five more eggs had been laid. However, I was not certain that both of these sets were laid by the same female, as competition for these burrows was keen. Lunk believed replacement nestings to be common in Michigan.

FLEDGED YOUNG

On the afternoon of 11 June 1976, three fledglings that had left the motmots' burrow no more than four or five days earlier, rested on naked twigs at the very top of the dead guava tree in front of the house, where their parents passed so much time between breeding seasons. Here they stretched, preened, scratched their heads by raising a leg over a lowered wing, and called with harsh twitters. Both parents fed them frequently, usually delivering the food while poising for an instant in the air in front of a perching fledgling, which received the meal with fluttering wings. At intervals the young swallows circled around briefly but competently, apparently already catching insects. For a few minutes two perched almost in contact on a leafless twig, but soon they moved apart to their usual distance of more than their own width. They already maintained their "individual distance."

I watched to see what these young Rough-wings would do as the day

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ended. Until late in the afternoon the three remained in the guava tree and were fed many times. At 16:55 many Rough-wings passed, circling overhead, apparently on their way to roost in large companies in a field of sugarcane, as I earlier described (Skutch, 1960). At 17:13 two of the young disappeared, but one stayed in the treetop, receiving more food from both parents. At 17:23 another group of Rough-wings passed by, and this third young swallow apparently followed them. For the next half-hour the parents continued to trace irregular courses above the pasture, lower than they usually flew in full daylight, mostly below the treetops and sometimes little higher than my head. One alighted in the guava tree with insects in its bill but found no young to receive them. With only brief rests in this tree, both parents continued to catch insects in the fading light until 17:52, when one of them joined another group of swallows flying westward. The other parent remained four minutes more, then departed westward as night descended. Thus, the young went to roost without their parents and the parents went separately. It is most unlikely that the family was reunited in the canefields where multitudes of Rough-wings roosted. How different from the behavior of Blue-and-White and other swallows that sleep in family groups long after the young fledge!

On the following afternoon, after the hardest downpour, I saw only two young Rough-wings in the guava tree, where the parents fed them. On the next two days I sometimes found the three together, still often fed by the adults. Thereafter, I saw no more of the juveniles, although the parents continued to frequent the dead guava tree.

In the following year, 1977, I made a longer series of observations on the behavior of young Rough-wings. On the morning of 30 May, the parents were still carrying food to the motmots' burrow, although I could not see the nestlings, which retreated around the curve of the long tunnel when I looked in. In the cloudy mid-afternoon of this day I noticed three fledglings perching, a few centimeters apart, high in a tall dead tree above the burrow they had just left. Presently they moved to another twig, where two rested in contact, with the third a few centimeters away. Soon the latter alighted on the backs of the other two, apparently trying to push in between them. Not succeeding, it flew to a nearby branch. At intervals the parents fed the fledglings, which sometimes made circling sallies, returning to the same high treetop. Here they stayed until 16:35 when a Garden Thrush (*Turdus grayi*) alighted near them and the trio flew beyond view. Their parents remained near the burrow.

Later the three fledglings perched in contact on a slender twig at the top of the dead guava tree in front of the house. Two faced in one direction and the third the other way. Beneath a slow rain falling from a darkly clouded sky, the parents brought them an occasional meal until about 17:15. Then the adults vanished, leaving the three young perching in a compact mass on the high, fully exposed twig, beneath the continuing drizzle. Long after nightfall I could still detect them through my binoculars as a dark thickening on the thin twig, silhouetted against the overcast sky, above which

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the moon shone. Fortunately for them, owls are extremely rare in this valley, and they came safely through the night. At dawn they were in the same spot, as closely pressed together as at nightfall. In roosting in contact on a twig these swallows resembled fledgling flycatchers of several species which, however, choose more sheltered perches amid foliage (Skutch, 1960). The only other small bird that I have known to roost in such an exposed situation is the Long-billed Starthroat Hummingbird (*Helimaster longirostris*) (Skutch, 1972).

I did not again find the young swallows sleeping in a treetop. Probably, after their second day in the open they went to roost in a canefield, as the brood of the preceding year had done. As this day ended one or more Rough-wings flew repeatedly in front of the motmots' burrow, or alighted momentarily at the entrance but, as far as I saw, none went in. Nevertheless, this behavior was significant, as it suggested that Rough-wings retain a vestige of the habit of returning to the nest to sleep, as certain other swallows do.

On 1 June the three young Rough-wings, only two days out of the burrow, were already meeting their parents in the air, receiving food while the two hovered breast to breast. If they could do this they probably could catch a few insects for themselves. After their first day in the open I no longer found them resting in contact, but always at least a few centimeters apart.

During the succeeding weeks I repeatedly saw young swallows being fed, sometimes in the guava tree, sometimes high on other dead trees nearer their burrow. As the juveniles grew older they increasingly met their parents in the air to take their food, instead of waiting for it on a perch. As late as 24 June I found five swallows circling above the pasture near the dead guava tree. Thrice two came together face to face, evidently transferring food in the air. At intervals one rested at the top of the guava tree. This was the last time that I saw a parent feed a juvenile. Although I lacked proof that the young that I saw being fed on 24 June were those who had left the motmots' burrow on 30 May, the continuity of my observations, and the persistent use of the guava tree for resting, point strongly to the conclusion that the same young swallows received some food for at least 25 days after they left the nest, or until they were about 43 days old. Yet these and other Rough-wings that I have watched have appeared capable of catching insects only a day after their first flights. In Texas Brown (1978) saw Purple Martins (*Pogone subis*) catch insects on their fourth and fifth days out of the nest; and by their seventh to tenth days the juveniles appeared to be independent of parental care. In general, tropical birds are attended by their parents longer than those at higher latitudes.

After 24 June the young Rough-wings, if still in view, were no longer distinguishable from adults. Thereafter I rarely saw more than the mated pair in the guava tree, which they continued to frequent until the approach of the following breeding season, as already told.

ROUGH-WINGED SWALLOW

SUMMARY

In Costa Rica Rough-winged Swallows may pair as early as September or October, and some pairs appear to remain intact throughout the year.

Year after year Rough-wings nested in an old motmots' burrow, and in short tunnels made specially for them in a roadside bank. Pairs competed keenly for these burrows, sometimes continuing to chase each other for several days.

Sets of four or five eggs were laid in April, more seldom in May, exceptionally in the first week of June. Eggs are usually laid on consecutive days, but rarely a day is skipped.

Incubation is by the female only. She may begin to pass the night on the nest before she starts to lay. Unlike other swallows, male Rough-wings seem never to roost on or beside the nest. The incubation period is 16 days, rarely a day or two longer.

Although males regularly feed nestlings, they may not begin until three or four days after the young hatch. The female broods at night only until the nestlings are seven to nine days old, although they are still largely naked.

In Central America the nestling period is 18 to 21 days, as in Michigan. Fledglings do not return to roost in their burrow.

Second broods are unknown in Central America, and even replacement broods appear to be rare.

On their first night out of the nest, three fledglings roosted, without their parents, in a compact mass on a high, fully exposed perch, beneath a drizzle. After this the young appeared to join passing flocks of Rough-wings on their way to roost in fields of sugarcane. The parents went separately.

After their first day in the open fledglings no longer perched in contact but maintained their "individual distance."

As soon as they leave the nest Rough-wings fly well, and a day later they appear capable of catching volitant insects. One brood continued to receive food from their parents for at least 25 days after they left the nest, or until they were about 43 days old.

Comparison of the breeding biology of resident Rough-winged Swallows in Central America and their migratory conspecifics in Michigan shows many similarities.



FIG. 8. Riverside Wren, *Thryothorus semibadius*.

Family TROGLODYTIDAE

RIVERSIDE WREN

Thryothorus semibadius

Bright chestnut above, conspicuously cross-barred with black and white on all the ventral surface except the white throat, with the sides of the head boldly streaked black and white, the Riverside Wren is one of the most handsome, easily identified members of its family. It has a restricted range on the Pacific slope of southern Costa Rica and the adjacent Province of Chiriquí in Panama, where it is found chiefly along rivers, at the wooded margins of swamps, on precipices overgrown with shrubs and vines, and in lush thickets from sea level up to about 1,200 m. Throughout the year these wrens live in pairs or family groups of three or four. Sounding above the clamor of tumultuous mountain torrents, their powerful, clear, ringing notes, in a variety of short phrases, help to keep the members of a family together while they hunt insects amid tangled vegetation, where they are not easy to glimpse.

The bulky globular nest is balanced over a slender horizontal branch above a stream, over its bank, in a neighboring thicket, or sometimes in an isolated tree in a clearing, not far from water. Standing unconcealed I have often watched both members of a pair build; but they seem invariably to abandon unfinished the nest where they have been seen at work. The completed structure, composed of fibrous materials and much green moss, consists of a well-enclosed chamber that is entered through an antechamber or vestibule almost equally spacious. The wide doorway of the antechamber faces downward and inward. Similar nests are used for breeding and sleeping, but the dormitories are often less carefully made. The wrens may sleep singly or in family groups of two or three, probably consisting of a female and her young.

When I wrote my earlier account of this wren (1960) I had found only two accessible breeding nests, and I did not know the incubation period. Since then I have seen four more nests with eggs or young. All six nests were low, ranging only from 1.5 to 2.2 m above the ground or river bank; four were 1.8 m up. Each of these nests contained two eggs or nestlings. The eggs are white, finely speckled with cinnamon or pale brown, chiefly in a cap or wreath at the thicker end, sparingly elsewhere. On some eggs the specks of color are barely visible on the white surface. The measurements of seven eggs average 21.4 by 15.2 mm. Those showing the four extremes measured 22.2 by 15.9, 20.6 by 15.1, and 20.7 by 14.8 mm. In six nests in the Valley of El General, eggs were laid as follows: February, 1; July, 3; August, 1; December, 1. Parents fed fledglings in September and October.

In a nest 2.2 m up in a young orange tree in a pasture, about 30 m from a creek, a Riverside Wren slept for at least a week before the first egg appeared. It was difficult to make this wren leave her eggs in the

RIVERSIDE WREN

daytime so that I could inspect them. She continued to sit while I shook the branch that supported her nest and even tapped on the nest's bottom. Such tight sitting is usual with Riverside Wrens. At this and other nests I could look in at the incubating or brooding wren with my head hardly more than 30 cm from her curiously striped face. I might have caught her in the nest had I so desired. A moderate amount of shaking could not make one wren leave her nest, but if I passed a twig or foliage across her doorway she promptly jumped out and, remaining nearby, scolded harshly. Riverside Wrens are almost equally reluctant to leave their dormitories after they have retired in the evening.

On 29 July 1970 I passed the morning watching a wren incubate in a nest situated 1.8 m up in a young rose-apple tree at the edge of a pasture, beside a huge rock that separated it from a creek. As far as I could tell, only the female sat in the nest. Rarely I heard the male sing by the neighboring stream; and once, during her recess, the female sang with him. While in the nest, she was always silent. The male did not approach the nest until the end of the morning, when he accompanied his partner as she returned from an outing. On this occasion he looked into the nest while she waited nearby. When he rejoined her she entered to resume incubation. Then he went again to look into the nest, lingered close to it for a few minutes, and returned to the creek.

This female first left her nest at 5:45 and by 11:51 she had taken three recesses, lasting 64, 65, and 49 minutes. The intervening sessions continued for 99 and 89 minutes. Thus, at the middle of the incubation period this wren incubated for only 51.3 per cent of the morning. At a nest which I watched for four hours in July 1942, the wren took two sessions of 67 and 69 minutes, and two recesses lasting 35 and 37 minutes. Long sessions, long recesses, and low incubation constancy appear to be typical of wrens of the genus *Thryothorus*, including the Rufous-breasted Wren (*Thryothorus rutilus*) (p. 156) and the Striped-breasted Wren (*Thryothorus thoracicus*) (Skutch, 1972).

When found on 20 July the nest beside the great rock held two eggs, which appeared to have been newly laid. On three visits that day I found them cold. One egg hatched between the afternoon of 7 August and 6:30 next morning, after at least 18.5 days of incubation. The second egg contained a small dead embryo. On 13 July 1972 I found a nest 1.5 m up in a tangle of vines and branches in the top of a fallen tree in the midst of a small banana plantation, about 36 m from a rocky side channel of the Río Peñas Blancas—farther from a stream than any other that I have seen. This nest already contained two eggs, of which one hatched on 30 July after at least 17 days of incubation. Again the second egg failed to hatch. Another wren incubated unhatchable eggs for at least 24 days. A long incubation period is usual in tropical wrens of woodland and thickets. That of the Chinchirigüí, or Plain, Wren (*Thryothorus modestus*) and of the Lowland, or White-breasted, Wood-Wren (*Henicorhina leucosticta*) is 18 days; and one determination of the incubation period of the Highland, or Gray-breasted,

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Wood-Wren (*Henicorhina leucophrys*) was 19 or 20 days. The Southern House Wren (*Troglodytes aedon musculus*), however, hatches its eggs in only 14 to 16 days (Skutch, 1953).

The newly hatched Riverside Wren has pink skin, wholly devoid of down, as in other tropical species of *Thryothorus*, including the Rufous-breasted, Striped-breasted, and Spotted-breasted (*Thryothorus maculipectus*) wrens. This condition is not universal among wrens, for species of *Troglodytes*, *Henicorhina*, and *Campylorhynchus* bear sparse natal down. In all wrens, as far as I know, the interior of the mouth is yellow. Because of the premature loss before hatching of all but one of the Riverside Wrens' nests that I found, I have only one determination of the nestling period, which was 16 days, the same as that of the Rufous-breasted and Striped-breasted wrens, for each of which I have a single determination. Although I have been unable to watch, amid dense thickets, newly fledged Riverside Wrens as night approaches, observations given above suggest that the parents lead them to sleep in a nest other than that in which they were raised.

On a bright sunny morning in mid-January I found, in a thicket beside a river, a Riverside Wren that resembled an adult except for the conspicuous yellow corners of its mouth. It was singing a rambling sequence of clear, soft, at times warbled notes, very different from the loud, ringing notes of adults. It reminded me somewhat of a canary. At times this juvenile gave a softer version of the bell-like notes of adults. This sweet, leisurely singing continued for many minutes, while the young wren hunted through tangled vegetation.

SUMMARY

The conspicuously marked Riverside Wren lives chiefly along the margins of streams, on precipitous slopes overgrown with shrubs and vines, and in lush thickets not far from water. In pairs or family groups of three or four, it searches for insects amid low, tangled vegetation.

The nest, a bulky globular structure of mosses and fibers, entered through a wide antechamber, is usually situated from 1.5 to 2.2 m above or beside a stream, or sometimes in an isolated tree in a nearby pasture. Both sexes build. The few available records suggest that breeding continues through most, if not all, of the year.

Two finely speckled white eggs are laid and incubated by the female, which takes the long sessions, long recesses, and achieves the low constancy typical of tropical wrens of the genus *Thryothorus*. The incubation period is 18 or 19 days.

The young, hatched without natal down, remain in the nest 16 days, after which they sleep in a dormitory nest.

Juveniles sing a soft, sweet, rambling song, very different from the loudly ringing, bell-like notes by which adults make themselves heard above the clamor of mountain torrents.

RUFOUS-BREASTED WREN

RUFOUS-BREASTED WREN

Thryothorus rutilus

Thirteen centimeters long, the Rufous-breasted Wren is plain brown on back, rump, and wings, more rufous on the crown, which is narrowly bordered with black. The grayish brown tail is barred with black. Below the white superciliary stripes, the whole cheeks, sides of neck, and throat are black, finely and densely spotted with white. The breast is orange-tawny, which color becomes paler on the more posterior underparts. The slender bill is black; the eyes are deep brown; and the legs and feet are dark. The sexes are alike.

From the central and southern Pacific slope of Costa Rica, the Rufous-breasted Wren ranges through much of Panama to northern Colombia, northern Venezuela, Trinidad, and Tobago. Altitudinally it extends from the lowlands up to at least 1,200 m in Costa Rica, 1,700 m in western Panama (Ridgely, 1976), and also about 1,700 m in Venezuela (de Schauensee and Phelps, 1978). Although abundant in the Valley of El General wherever tall, lush, vine-laden thickets or liana-draped forest edges remain, this wren is so secretive that the life history which I published in 1960 contained large gaps. In the following years I have continued to live where almost daily I hear the antiphonal singing of a mated pair (as I do while I write this), and I have learned a little more about this wren. Nevertheless, my knowledge of its life history remains less complete than that of many a bird even less abundant at Los Cusingos.

FOOD

As far as I have seen, the Rufous-breasted Wren is wholly insectivorous, restlessly searching for insects and spiders amid concealing foliage and dead leaves caught up in vine tangles. At times it attacks surprisingly large insects. One morning in July I noticed a Rufous-breasted Wren standing on the ground amid short herbage by our water tank. The bird had caught a big, grasshopperlike insect that it was pecking and tearing to pieces. At intervals it swallowed a fragment but, after I had watched for about five minutes, the major part of the orthopteron's body was still intact. Then the wren stood motionless on the ground for several more minutes, as though recovering from its strenuous exertions. Finally it picked up what was left of the insect and flew away.

This wren's behavior seemed reckless and uneconomical. Instead of remaining safely within the sheltering tangles where it is most at home, it stood for a considerable interval in an exposed situation, where a predatory bird or mammal might easily have surprised it. And while struggling with too large a prey, it might, with less expenditure of energy, have caught several smaller invertebrates that together would have supplied about as much food as the single big one. Doubtless small birds do best to hunt small insects.

RUFOUS-BREASTED WREN

VOICE

The earliest singing of many songbirds consists of rambling medleys, often sweeter and more prolonged than the adults' songs but lacking the distinctive character that serves to identify the species. This is outstandingly true of wrens, whose adult songs are often short, clear-cut, and exquisitely modulated. In early August 1970 a young wren, that frequented our garden with its parents, repeated softly warbled, rambling songs, without definite phrasing, that appeared to be its first attempts to sing. As the days passed its singing became longer and stronger, until it reminded me of the prolonged, indefinite songs of the Highland, or Gray-breasted, Wood-Wren (*Henicohina leucophrys*). Now I sometimes heard what appeared to be attempts to produce the clear, sharply defined phrases of five or six notes that its parents so often sang; but its voice was much softer than theirs and it had not mastered the modulations. These juvenile songs continued for at least seven weeks. Sometimes two young wrens sang softly and sweetly while the parents answered each other with briefer, sharper phrases. The hunger call of these young wrens was a high, sharp monosyllable.

In 1966 I found this widespread species lurking amid vine-tangles in second-growth woods near Pirapira, at about 400 m above sea level in Carabobo, Venezuela. Its song was surprisingly different from any that I have heard during more than four decades of familiarity with the Rufous-breasted Wren in Costa Rica. Two full, prolonged whistles, or sometimes three shorter notes, introduced a liquid trill or quaver. I have never heard a trill from a Rufous-breasted Wren in Costa Rica. Each time that I heard this beautiful song in Venezuela I listened in vain for the answering notes of a mate. In April the few Rufous-breasted Wrens that I met in this locality appeared to be alone. Perhaps the females were in their nests.

ALLOPREENING

In a letter dated 2 July 1975, Patty O'Brien told me of an instance of allopreening by Rufous-breasted Wrens that she had watched in the Santa Marta region of northern Colombia. While two wrens, probably a mated pair, perched facing each other on a barbed-wire fence, one made the feathers of its head and neck stand on end, while the other pecked at the top of its companion's head. Doubtless because of their secretive habits, wrens have not often been seen to preen or groom their associates. In Panama Eisenmann (1950) watched an adult Buff-breasted Wren (*Thryothorus leucotis*) work with its bill over the top of the head and back of an almost full-grown young bird that it had been feeding, as if searching for vermin or preening the feathers of its offspring. In the Guatemalan highlands I watched a pair of Banded-backed Wrens (*Campylorhynchus zonatus*) alternately preen each other's plumage and their own (Skutch, 1960). In widely separated localities in Mexico, Elliott and Davis (1965) each witnessed allopreening by the closely related Gray-barred Wren (*C. megalopterus*), and

RUFOUS-BREASTED WREN

I have seen it in the congeneric Rufous-naped Wren (*C. rufinucha*). Some years ago I watched a Lowland, or White-breasted, Wood-Wren (*Henicorhina leucosticta*) that seemed to pick something, possibly a tick, from amid the plumage of its mate's head.

SLEEPING

In my earlier account of the Rufous-breasted Wren (1960), I told how I had found a single individual sleeping in a well-made, globular nest with a round doorway in the side, 1.7 m up in a tangle of vines in a brake of tall wild cane (*Gynerium sagittatum*). Two other wrens lodged singly in exceedingly flimsy pockets, composed of grass, rootlets, and moss, one 3 m up and the other 7.5 m above the ground. These nests appeared to be unfinished, or disintegrating, dormitories of the Bananaquit (*Coereba flaveola*); in one of them a Bananaquit was later found sleeping. Surprisingly, several substantial nests, newly built by the wrens themselves, were, as far as I could learn, used neither for breeding nor for sleeping; and nests from which a brood had just departed were not occupied at night by either the parent or the young.

In later years I gathered much additional evidence that Rufous-breasted Wrens frequently lodge in nests that they have not built. In mid-April 1957 I found a wren sleeping in a nest apparently built by a Bananaquit, 3 m up in an orange tree in a pasture. It rested with its tail outward. On the following evening a Bananaquit emerged from this nest, which the next day collapsed beneath heavy rain.

On 15 February 1960 I watched a Bananaquit build a nest 3 m up in a lemon tree in front of the house. In the evening of the same day I found the Bananaquit flitting nervously around its new nest, uttering sharp notes, instead of entering. A Rufous-breasted Wren was already comfortably installed within! The intruder flew out as I approached to investigate, but after much churring and fidgeting it returned a few minutes later to sleep through the night with its orange-tawny breast filling the doorway.

After the wren entered the Bananaquit's nest on the following evening, the latter flitted around it with sharp calls but did not try to enter. Then the wren's mate went at least six times to the doorway, as though to join the other inside, but each time it promptly left. I could not see whether the wren inside repulsed with pecks the wren outside, that finally went elsewhere for the night. This was evidently the male of the pair, for he had the fuller song.

The next evening the Bananaquit arrived at its nest before the wren. The tiny, yellow-breasted bird flitted around, went several times to the doorway, and once appeared to enter, only to leave in less than a minute, as though it feared to be caught there by the wren. Presently the latter came and entered. A little later the Bananaquit again approached the doorway. The wren grappled with it. I heard low squeaks that seemed to come from

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the smaller Bananaquit, then the latter flew away. Thereupon the wren left the nest but soon returned to sleep with its head in the round entrance. On the next two evenings, however, the Bananaquit entered its nest for the night with no interference by the intruder. Nevertheless, its troubles with the wren were not over. On several evenings in mid-March, a month later, I found the Bananaquit in the nest, but after nightfall the wren was always sleeping there. By the month's end the Bananaquit was occupying its dormitory. Such alternating occupancy of a Bananaquit's nest by the builder and an intruding Rufous-breasted Wren is not unusual. In May of the following year I found still another instance of it.

The Rufous-breasted Wren also occupies nests made by wrens of other species. In October 1969 a Riverside Wren (*Thryothorus semibadius*) started to build in a grapefruit tree but, as often happens, never finished its nest. On rainy nights in November a Rufous-breasted Wren slept in this flimsy, thin-roofed structure.

In the absence of an available nest built by some other bird, the Rufous-breasted Wren may use shelters of other kinds, including large tank bromeliads with broad, strap-shaped leaves arranged in a tight rosette. In July 1970 one of these wrens slept on a lower leaf of such a bromeliad growing on a calabash tree in front of our house. Pushing far in against the base of the rosette, the small bird was in a snug niche, well shielded by all the leaves above from the heavy nocturnal rains of this season, but visible from outside. On the dark, rainy afternoon of 20 July the bird retired into its nook as early as 17:30, well before nightfall. While one wren entered the bromeliad, its mate slipped into a pocket in a brown, fluffy mass of the liverwort *Frullania*, at the end of a long branch on the opposite side of the same calabash tree. In this tree Tawny-bellied Euphonias (*Euphonia imitans*) also slept in niches amid the profuse growth of liverworts, often in pockets that were cozier than that chosen by the wren (Skutch, 1972). Two years later, in May, a Rufous-breasted Wren slept, with its tail projecting outward, in the niche where a female euphonia formerly lodged. The opening of this pocket had been narrowed with material brought by a Bananaquit. Near the wren two male Tawny-bellied Euphonias slept in similar pockets amid the liverworts.

Although Southern House Wrens (*Troglodytes aedon musculus*) and other species of *Troglodytes*, which nest in holes and hollows, roost in the most varied nooks in man-made structures or natural sites, other wrens that are skillful builders regularly occupy dormitories that they have made for themselves. Like other species of *Thryothorus*, the Rufous-breasted Wren builds cozy covered nests but, unlike its tropical congeners for which I have information, it appears to prefer to sleep in nests, however skimpy, built by other birds, or in such nooks amid vegetation as offer a modicum of shelter. As far as I can learn, it always sleeps alone and at nightfall does not install its fledglings in a nest or other shelter—in this, too, differing from other wrens.

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NESTING

Nests are built by both sexes, working together or one at a time. In my earlier account of the Rufous-breasted Wrens I reported having seen them build at heights up to 12 m or somewhat more in vine tangles, and attending eggs or nestlings in nests ranging from 4.5 m to only 10 cm above the ground. Such low nesting by this wren was surprising, but subsequent discoveries showed that it was not as unusual as it at first seemed. On 14 June 1976 I found an occupied nest 13 cm above the ground in an open, grassy space at the northern end of our garden, where it was supported, but not sheltered or concealed, by low weeds. It was close beside a large orange tree whose lower leafy branches reached the ground. On 7 June 1977 another low nest was discovered about 15 m from the site of that of the preceding year. This nest was 25 cm above the ground, in the midst of a dense, leafy clump of the vigorous monocotyledonous herb *Alpinia purpurata*, as well concealed as its predecessor was exposed. Nevertheless, it was no more successful.

These nests were bulky covered structures, measuring about 13 cm high, 13 cm from front to back, and 15 cm wide. The round doorway in the side was 4 cm in diameter. They were composed of dry weed stems, grass blades, and fragments of decaying fronds of a nearby African oil palm (*Elaeis guineensis*). The lining was of finer materials.

Each of these nests held three eggs. Those in the first nest were faintly tinged with buff and had fine cinnamon speckles concentrated on the thicker end, more sparingly scattered over the remaining surface. The eggs in the second nest were more heavily pigmented on a dull white ground. Speckles and blotches of reddish brown lay densely over the whole thick end and were thinly scattered elsewhere. On other eggs brown spots form a heavy wreath around the thicker end. Including the foregoing, six nests held 3 eggs or nestlings, and one nest had 2 nestlings. The measurements of eight eggs average 17.9 by 14.0 mm. Those showing the four extremes measured 18.3 by 13.9, 17.5 by 14.3, and 17.5 by 13.5 mm. A set of three fairly fresh eggs weighed 4.9 g, or approximately 1.6 g each.

In 10 nests in the Valley of El General, eggs were laid as follows: March, 3; April, 2; May, 2; June, 1; July, 2. Two stubby-tailed fledglings that I saw a pair of Rufous-breasted Wrens feeding on 26 February 1937 were hatched from eggs laid in January. The latest nest held young well into August. In Trinidad and Tobago sets of two to four eggs were laid in 21 nests from January to July (French, 1973).

Since I lacked observations on nest attendance before the eggs hatched, I passed the morning of 16 June watching the female incubate in the nest in the open grassy area beside the orange tree. In the dim light of dawn, while Garden Thrushes (*Turdus grayi*) filled the air with liquid melody, I entered the blind. At 5:21 a small bird, not clearly identified in the dim light but doubtless the male wren, alighted on the nest's roof, whereupon the female left, followed by the other. At 6:00 the pair of wrens approached,

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singing antiphonally. The female descended through the dense foliage of the orange tree, scarcely revealing herself. As she neared the nest she stopped singing. Entering, she settled on her three eggs facing outward, her usual orientation. Her mate sang a few more times, then vanished. After incubating for 40 minutes she left, flying straight out over the open lawn. When she returned 51 minutes later she brought a billful of seed down that she deposited in the nest as she settled down to warm her eggs.

By noon the female had taken four recesses, lasting 39, 51, 52, and 45 minutes. Her four sessions continued for 40, 63, 57, and 57 minutes. The last was ended when a cock flapped his wings and crowed loudly near the nest. She incubated for only 54 per cent of the sunny morning. On each return to the nest, except the first, she brought seed down or fibrous material (three billfuls in all) to add to the lining. During her last session of the morning she closed her eyes and drowsed briefly. Once in the course of every session, except the first, her mate came near and sang profusely; 45 times during her second session, 43 during the third, and 35 times during the fourth session. While in her nest the female was silent.

Two days later this nest lay a meter from its original site, and the eggs had vanished. The absence of feathers suggested that the female had escaped unharmed, to nest the following year in the clump of *Alpinia purpurata*, where she hatched three pink-skinned nestlings, wholly devoid of down, and with yellow inside their mouths. They survived only a few days. As a result of such losses, I am unable to give the incubation period, which is probably about 18 days, as in other species of *Thryothorus*. The nestlings, fed by both parents, remain in the nest for 16 days, as in the related Riverside (*T. semibadius*) and Striped-breasted (*T. thoracicus*) Wrens. When the eggs in the lowest of all the nests that I have seen were on the point of hatching, the female jumped from it at my approach and fluttered over the ground for several meters, with spread tail and beating wings, in a fairly convincing distraction display, the only one that I have seen in any wren.

SUMMARY

Living throughout the year in pairs that keep in contact by antiphonal singing as they forage through tall, lush, vine-laden thickets or the liana-draped forest's edge, Rufous-breasted Wrens inhabit the Tropical Zone up to about 1,200 m in Costa Rica and 1,700 m in Panama and Venezuela.

Their food consists of small invertebrates that they seek amid living foliage and dead leaves caught up in vine tangles. Sometimes they attack insects too large for them.

The softly warbled, rambling songs of young wrens gradually develop into the short, sharply defined phrases which adults sing antiphonally.

Songs of Rufous-breasted Wrens in Venezuela differed greatly from those of the same species in Costa Rica.

Allopreening has been reported in this and a few other wrens.

Although Rufous-breasted Wrens build substantial covered nests, they

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often neglect to use them but sleep in flimsy structures made by other wrens or Bananaquits. Sometimes they roost in niches amid clustered liverworts or under the leaves of tank bromeliads. Rufous-breasted Wrens and Bananaquits may alternately lodge in the same nest built by the latter. Adults were always found sleeping singly. Apparently, fledglings are not led to sleep in a nest.

Both sexes build the nest from 10 cm above ground amid herbage to 12 m or more high in vine tangles. Eggs are laid from January to July, but chiefly from March to July in the Valley of El General. The most frequent set consists of three eggs, with two and four reported elsewhere.

Only the female incubates, taking long sessions separated by long recesses. One female covered her eggs for 54 per cent of a sunny morning. Returning to resume incubation she brought material to add to her nest. The incubation period has not been determined but is probably 18 days, as in related wrens.

The nestlings are fed by both parents and remain in the nest for 16 days.

The only distraction display by any wren that I have seen was given by the female that had the lowest nest.





FIG. 9. Garden Thrush, *Turdus grayi*.

Family TURDIDAE

GARDEN THRUSH

Turdus grayi

A bird familiar to many people acquires many names. Costa Ricans, who know *Turdus grayi* better than any other small bird, call it *yigüirro*, and have chosen it as their national bird, a distinction that it has won by its profuse, melodious singing rather than by its very plain plumage, brownish olive above and buffy brown below. North Americans resident in Central America often know it as the "tropical robin." In earlier writings I have, for lack of a better name, called it simply "Gray's Thrush." In much recent literature it is designated "Clay-colored Robin"; but this is hardly enlightening, for clays vary in color from red to blue. Although I am reluctant to burden the literature with another name, a bird so well known and loved by English-speaking people, as well as by the natives of the countries where it resides, certainly deserves an English name that is appropriate. Accordingly, I propose to call it the "Garden Thrush." No other bird is so conspicuous, to ears as well as eyes, in gardens and dooryards throughout much of continental Middle America. And "thrush," the long-established English name for species of *Turdus*, seems more fitting than "robin," a name which traditionally belongs to a red-breasted Old World bird of a different genus.

From both coasts up to about 2,150 m, the Garden Thrush is widely distributed from northern Colombia to northeastern Mexico, and an occasional individual reaches southern Texas. In Costa Rica I have met it as high as 2,450 m and found it nesting freely around 2,150 m. Carriker (1910) recorded a nest at 2,450 m. Even in semi-arid regions it is present amid the lush growth along river bottoms and in irrigated plantations. Everywhere it prefers gardens, parks, plantations, shady pastures, and light, open woods to heavy forests, where the White-throated Thrush (*Turdus assimilis*) is more likely to be found. Nevertheless, it is much more conspicuous around human habitations while it is singing and nesting than after the breeding season.

When family cares are over, many Garden Thrushes seek more secluded areas where food is abundant. Although I have only once, in Honduras many years ago, found a Garden Thrush nesting even a short distance within primary forest, I often meet them well within the forest at Los Cusingos, visiting fruiting trees or foraging on a muddy pathway—never however, more than a few hundred meters from a clearing. In the Motagua Valley of Guatemala, early in the year, before nesting began, I found these thrushes living in quiet secrecy among willow trees and giant canes on low, marshy ground between a banana plantation and a tributary stream. When foraging over the ground beneath sheltering vegetation they are wary and difficult to watch. Even when they nest in dooryards they are less confiding in man than the American Robin (*Turdus migratorius*), doubtless because they

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have not been so well protected. Around our house they have become somewhat less shy after years of freedom from persecution.

Alighting after a long or short flight, Garden Thrushes twitch their tails vertically while they rapidly spread and close the brown feathers laterally, a double movement that attracts attention whether one views them from behind or from the side. They are essentially solitary birds that I have never seen flying in flocks. Even when several visit a fruiting tree they come and go independently. If they retain the same mates from year to year, the two certainly do not keep close company. However, a number may roost in the same widespreading clump of tall timber bamboos, with many birds of other kinds. On a night in early March, as the nesting season approached, my flashlight's beam picked out two, evidently a mated pair, roosting in a small orange tree in a coffee plantation. They slept about a meter apart, on slender, rather exposed branches 2 and 2.8 m above the ground. When I first noticed them, their heads were exposed rather than turned back and hidden amid their plumage.

FOOD

Like other species of *Turdus*, Garden Thrushes forage much on the ground, where they hop along with feet together and push aside litter with their bills. Those that I have watched have preferred shaded spots to open lawns and pastures. From the moist ground they gather worms, slugs, insect larvae and pupae, and occasionally they capture a small lizard. Although mostly they forage alone, sometimes they join a variety of birds to take advantage of the invertebrate fugitives from army ants. Once, in light, open woodland near heavy forest, I watched a thrush collect fugitive insects until it flew away with a billful, evidently for nestlings.

Fruits of many kinds enter prominently into the Garden Thrush's diet, Frantzius (1869) long ago recorded its fondness for small wild figs. It eats many small berries of *Miconia* spp. and other trees and shrubs of the melastome family, and the larger red berries of *Hamelia patens*, a weedy shrub of the coffee family. These thrushes join many other birds, from tanagers to toucans, in plucking pieces from the green fruiting spikes that dangle in fingerlike clusters from the thick boughs of *Cecropia* trees. They prefer to swallow fruits whole, seeds and all, rather than peck into them. When they enter the forest to share the berries of the small or middle-sized cacique tree (*Myrciara floribunda*) with Brown-headed Parrots (*Pionopsitta haematotis*) and Rufous Pihas (*Lipaugus unirufus*), they gulp down entire the pale red fruits, which are 10 to 11 mm in diameter, each containing one or two large seeds, 5 or 6 mm in diameter.

Another, still unidentified, myrtaceous tree very common in the forest at Los Cusingos, the arenilla, gives them more trouble. The many tanagers that eat these bright red fruits, from 12 to 45 mm in diameter, peck into them while they hang on the twigs. But the Garden Thrushes and White-throated Thrushes have not learned this simple procedure and, accordingly,

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are limited to the smaller fruits, which they eat along with the hard-shelled, apparently indigestible seeds, 7 to 10 mm in diameter. If one of these thrushes plucks a fruit too big to be forced down, it drops the berry and tries another. The Garden Thrushes often alight on the ground beneath a fruiting arenilla tree, but they are then so shy that I have not succeeded in learning whether they eat fallen berries. Even when quite ripe, the soft pulp of these fruits is astringent, like unripe persimmons, and it has scarcely any flavor.

When the tall wild nutmeg trees (*Virola Koschnyi*) in the forest open their two-valved fruits, exposing in each a single brown seed closely embraced by the branching arms of a bright red, oily aril, the Garden Thrushes' insistence upon swallowing the seeds whole, as bigger toucans and trogons do, limits them to the smaller ones which, measuring about 23 by 15 mm, they can force down only with great effort. However, in the keen competition to obtain the white arils of tall trees of *Dipterodendron elegans*, the thrushes peck fragments from between the valves of opening pods, although they prefer to swallow the shiny black seed with its attached aril. The smaller arillate seeds of *Alchornea latifolia*, *Davilla Kunthii*, *Souroubea guianensis*, *Lacistema aggregatum*, and *Clusia* spp., all of which are freely eaten, are more easily swallowed by the thrushes.

Shy and suspicious, Garden Thrushes did not come to eat the bananas and plantains on my feeder until more than two years after birds of other kinds had become habitual visitors. Apparently, scarcity of other foods in the severely dry month of March 1945 forced them to overcome their timidity and alight on the board in the guava tree beside the house. Even then they would continue to eat only if they were unaware that I saw them. Unlike most of the visitors of twenty-odd other species, they left abruptly when I appeared on the porch. If they saw me watching they lurked in the upper boughs of the guava, or in more distant trees, nervously calling *tock tock tock*. Later both parents began to carry billfuls of banana to their nest in a nearby shed, but they were still exceedingly cautious in approaching the board. Soon a young bird with spotted wing coverts was coming often to partake freely of the fruit, while it voiced sharp little notes.

As the years passed Garden Thrushes came with increasing confidence to the feeder, doubtless because some of them had formed the habit of visiting it while still young and relatively unsuspicious. They were not the most welcome guests, for by trying to remove big pieces from a banana they often pushed it from the board, and they threatened other diners with snapping bills. Sometimes, however, they permitted birds as small as honeycreepers to share the fruit with them, and they never tried to monopolize the feeder, as by keeping others away while they were not themselves eating. Although they threatened, I never saw them attack another bird except those of their own species. Not content with driving a second thrush from the table, the pursuer often chased it through neighboring trees, with shrill cries and the sound of wings striking loudly against foliage. Although no other visitors to the feeder have been so consistently aggressive, I never

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saw one thrush injure another. These encounters between thrushes were most frequent as the breeding season approached and while it lasted. After its conclusion the thrushes scattered more widely to seek food. Since a pair of thrushes often had a nest near the feeder, probably they were defending their territory when they chased other thrushes from the board situated within it.

VOICE

Unlike its persistently songful neighbor the Orange-billed Nightingale-Thrush (*Catharus aurantirostris*), but like its other neighbor, the White-throated Thrush, the Garden Thrush sings freely only just before and during its breeding season. Here in the Valley of El General its song is rarely heard in January, when the dry season begins. In the drier month of February it is almost as silent, although an unseasonable shower may stimulate snatches of song. In March, especially if showers break the drought, song increases as nesting begins. The association of singing with the advent of wetter weather is so evident that rural Costa Ricans say that the *yigüirro* is "calling the rains."

In April and May Garden Thrushes are in fullest song. As day dawns their many-voiced chorus floods the valley with liquid melody. As the bright sun rises high into a clear sky they tend to fall silent, to resume singing as the clouds, spreading outward from the high cordillera in the north, dim the intense tropical sunshine. On overcast, drizzly, or even showery afternoons at this season, so many Garden Thrushes sing so continuously in the cleared lands of the valley that so much sweetness begins to cloy. If May is very wet song decreases in volume and in June, as many pairs finish nesting, it wanes until in July it is infrequent. Through the remainder of the year one hears only a rare, brief outburst of song.

I shall not attempt to describe the Garden Thrush's long-sustained, richly varied outpouring of mellifluous notes. As with other birds that sing elaborately, there is much individual variation in songs, but at its best the Garden Thrush is one of the most gifted of songsters. Those who have heard the songs of both this thrush and the related American Robin have noticed their close resemblance but have judged the tropical thrush to be the finer minstrel.

As far as I know, only the male Garden Thrush sings. An incubating female uttered only a low, liquid note when her mate sang nearby. A throaty *tock tock tock*, variously inflected, seems to express uneasiness or mild alarm. When nest or young appears to be endangered and often, too, in other circumstances, adults voice a loud, querulous *keyoo*, the more excitable of them with annoying frequency. In the season when song is in abeyance, Garden Thrushes often begin the day with this mournful note. Rarely a thrush utters a thin, sibilant, lisping note of unknown significance, or a short, dry rattle. Parents urge sluggish nestlings to take their meals with a low *tuck tuck*.

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NEST

Site.—In 1968, after an unseasonably wet week, a thrush started a nest in our garden at Los Cusingos on the exceptionally early date of 22 February. Otherwise I have noticed no building here until March, and it hardly becomes widespread until the month is well advanced, or, in some years, not until April. The rather heavy nest requires a firm support, which is usually in a stout fork or amid close-set branches of a tree or shrub, preferably one with dense foliage, or one well draped with vines. Often, however, a quite different site is chosen. The cut-off top of a stump or living fence post, surrounded by ascending sprouts, offers a strong foundation, lateral support, and good concealment. Many nests in our garden have been placed at the bases of the broad, red-and-green leaves of the shrubby caña de India (*Taetsia fruticosa* var. *ferrea*) or of the long, slender, fleshy leaves of the itabo (*Yucca elephantipes*).

In a banana plantation the nest is often built upon the topmost, upturned "fingers" of a bunch of green fruit, which prevent its slipping off, while the small "protecting leaf" may form a green roof above it. Or the nest may be situated on the broad base of a petiole of one of the gigantic banana leaves, against the false stem, or on the elbow at the top of a banana trunk that has been nicked and doubled over to bring the heavy bunch of fruit within reach of the harvester. Two nests, precariously supported on long dead leaves strung between two banana stems of the same clump, fell before the nestlings fledged. The broad base of the massive petiole of a coconut palm's frond provides a firm support. Less secure was the broad, nearly flat top of a fanlike leaf of a Panama-hat plant (*Carludovica palmata*), held aloft on a long, slender petiole where, on her second attempt, a Garden Thrush succeeded in completing a nest and raising a brood, close beside a house in Panama.

Once I found a thrush building in a natural cavity 12 m up in the tall, straight trunk of an ojoche tree growing in a pasture. The fissure was so narrow that the builder had difficulty squeezing in and out, but it was long and permitted me to see the outer side of the nest and part of the thrush while she worked upon it. Four nests were built beneath the thatched roofs of open sheds, in one of which horses took shelter from rain. Twice, returning home after absences of several months, we found nests in the corners of broad window sills, against shutters that had remained closed. Rarely the abandoned nest of some other bird, including a dove, a Scarlet-rumped Tanager (*Ramphocelus passerinii*), and a Buff-throated Saltator (*Saltator maximus*), is occupied, after more or less building by the thrush.

Higher in rainy, cloud-bathed mountains where epiphytes in stupendous variety profusely burden trees and cover stumps, Garden Thrushes build amid the massed stems or roots of this aerial vegetation, where their nests are excellently concealed. One nest was set among the dead outer leaves of a small tank bromeliad that grew upon an erect trunk standing in a pasture. Surrounded and supported on all sides by the stiff, dry leaves

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of the rosette, the nest needed, and had, exceptionally thin walls. Also high in the mountains a nest was built in a deep pocket amid creeping grass that draped over the top of a vertical roadside bank 3 m high.

Just as the Garden Thrush builds its nests in a great variety of sites, so it places them over a wide vertical range. The lowest that I have seen was only 1 m above the edge of a steep bank, but much higher above the ground at the bank's foot. It rested upon a slender stump, amid concealing water sprouts. The highest was over 30 m, in a towering ojoche tree in a pasture. Nests above 9 m are rare. Three quarters of 100 nests were from 1.5 to 3.5 m up.

Building.—As I earlier (1960) reported, at six nests I saw only the female build. The only aid that a male gave to his toiling partner, other than the encouragement of his song, was to pick up a piece of moss that she had dropped on a nearby branch and take it to the nest. In 1971, however, I watched a more cooperative male in exceptionally favorable circumstances. While we sat at breakfast before sunrise on the last two mornings of April and the first of May, a male Garden Thrush came repeatedly to a certain spot amid the variegated foliage of a *Taetsia* shrub in front of the dining room window, where he remained for a minute or two and sang a few notes. Later in the day he sometimes repeated these visits. I never noticed anything in his bill and, after he left, I found no nest material where he had rested. Evidently he was choosing the nest site.

After this had happened on the third morning, both members of the pair started to build in this site, before 9:00 on 1 May. On this day, I also found them working at noon. They made eight visits to the nest before a thunderstorm blew up with hard rain. On the mornings of 2 and 3 May I watched for a total of six hours and 20 minutes, during which they brought material to the nest 167 times. In the hour of most active building, 8:00 to 9:00 on 2 May, they brought material 37 times; and from 7:00 to 8:00 on the following day it was brought 29 times. Although I could not distinguish the sexes except by voice, it was clear that both were building actively. When, as often happened, the two occupied the nest consecutively, only one ever uttered a musical syllable, from which I concluded that only the male sang. Usually he delivered only a few songful notes, but occasionally he sang more freely, answering other male Garden Thrushes that caroled nearby.

Not only did the male thrush bring much material, frequently he sat in the incipient nest for minutes together, arranging it. At first, when one partner, arriving with a contribution, found the other in the nest, it either dropped the material beside the other or carried it away, to return with it after the nest was vacant. After a while the bird in the nest learned to take pieces from its co-worker's bill. Even after this, however, a thrush arriving with material was often reluctant to pass it to the other. Each wanted to place and arrange its own contribution. Sometimes the bird arriving with a billful stood on the nest's rim until the other went or, growing impatient,

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it forced itself in beside its mate, which then left. Rarely one pulled material from the other's bill. For long intervals the nest was occupied continuously by the partners working there alternately. Even while the male helped actively, the female appeared to do the larger share. As the nest neared completion he tended to remain aloof, leaving his mate to carry on alone. Thus, from 15:00 to 17:00 on 3 May, when 13 billfuls were brought, I did not see two birds at the nest together, and I heard no song there. During these two hours males sang almost continuously in surrounding trees, even while rain fell slowly. Likewise, next morning, from 6:00 to 8:00, when 30 billfuls, mostly rootlets and similar materials for the lining, were brought, I saw nothing to suggest that the male was helping his mate.

These builders found on the ground most of their materials, including fibers, muddy plant fragments, and lumps of mud. Once the male carried up a piece of a green living plant longer than himself. They plucked green moss from trees.

This nest was evidently for a second brood. From time to time the builders fed a stubby-tailed fledgling that hopped over the lawn nearby, repeating a sharp *tsip*, and sometimes flew into the shrub where the nest was taking shape. While finishing her nest the female found time to pass bits of banana to the fledgling at the birds' table. Once one of the parents fed the youngster, then promptly gathered material and took it to the nest. Started before 9:00 on 1 May, this nest appeared to be lined and finished by 9:00 on 4 May, but a parent visited it occasionally later in the day.

Throughout the thrush family females appear mostly to build alone, although males sometimes help, even in species such as the American Robin and European Blackbird (*Turdus merula*), in which their participation in this activity is exceptional (Skutch, 1960). Like most thrushes of the Northern Hemisphere, the Cape Robin (*Cossypha caffra*) of southern Africa builds her nest alone (Rowan, 1969).

Finished structure.—The Garden Thrush's completed nest is a broad and relatively shallow open bowl, with walls that are usually massive. The outer layer may be composed largely of green moss or of coarse vegetable materials, that from some structures project untidily. Within this is usually a layer of mud or clay, mixed with fibrous materials that bind it together. This hard shell may not extend as high as the nest's rim. Within it is a lining composed of coarse rootlets, curving dry rachises of small compound leaves, the fungal rhizomorphs called "vegetable horsehair," and fibers of various kinds. In the wet weather when most Garden Thrushes nest the fragments of living plants that they incorporate in the walls, and perhaps also seeds that had fallen into the mud that they bring, often grow in the earthy layer, forming a green wreath around the rim. The most attractive of these aerial gardens that I have seen was that on the nest situated upon a leaf of the Panama-hat plant in Panama, where 10 cm sprouts of the chickweed *Drymaria cordata* grew among *Selaginella*, *Tradescantia*, *Peperomia*, and grasses (illustrated in Skutch, 1976:102). Other nests are adorned with living fronds

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of small ferns, in addition to moss that remains green. Nests measure 15 to 20 cm in diameter by 10 cm high. The interior cavity is 9.5 cm in diameter by about 5 cm deep.

In contrast to massive nests made early in the season, an exceptionally late one built in July was a flimsy structure. Upon a recently abandoned nest of a Scarlet-rumped Tanager, the thrush placed a fairly thick but narrow foundation layer of mud. Above this she built up walls of coarse, fibrous rootlets, with an admixture of rachises and plant fibers. Around the rim she placed a little green moss. Much light passed through the thin walls, which lacked the usual middle layer of hardened mud.

EGGS

In the exceptionally early nest begun at Los Cusingos on 22 February 1968, the first egg was laid on 3 March, but here few Garden Thrushes lay before the middle of the month. The nest which the male helped to build was started on 1 May, finished on 4 May, and received its first egg on 7 May. With rare exceptions eggs are laid on consecutive days. In contrast to tanagers and finches, which deposit their eggs early in the morning, Garden Thrushes often lay rather late. Of first eggs in nests I have known one to be laid before 6:35, another before 7:00, one between 7:00 and 9:00, and one between 7:00 and 10:08. The second egg follows somewhat more than 24 hours later. Of 10 second eggs none was laid before 6:55; one was laid between 6:55 and 8:00 and another between 7:10 and 8:40. Five were laid after 9:00, one of these 9:30–11:00, and another 11:15–12:15. Of seven third eggs none was laid before 7:00, but two were laid before 9:10. Three were laid after 10:15, but none was known to be laid after 11:20. Closer approximation of the time of laying could not be made without keeping the thrush from her nest, possibly when she was ready to lay. In southern Africa Cape Robins also lay successive eggs at intervals somewhat greater than 24 hours (Rowan, 1969).

Of 115 nests in Guatemala, Honduras and, chiefly, Costa Rica, 40 contained two eggs or nestlings, 72 held three eggs or nestlings, and 3, all in El General, had four eggs (average, 2.68). The eggs are pale blue, pale grayish blue, or, more rarely, bright blue, speckled and mottled all over, but most heavily on the thicker end, with bright rufous, rufous-brown, and pale lilac. An egg in one of the very few sets of four that I have seen was very faintly and sparingly marked, suggesting that the female's supply of pigment was almost exhausted when she laid it. The measurements of 37 eggs average 27.8 by 20.4 mm. Those showing the four extremes measured 31.0 by 20.6, 27.8 by 21.4, 25.4 by 20.6, and 25.8 by 19.4 mm. The weights of six newly laid eggs ranged from 6.1 to 6.9 g and averaged 6.4 g.

In 101 nests in the Valley of El General, eggs were laid as follows: March, 22; April, 39; May, 32; June, 5; July, 3. The latest of these nests, the slight structure built upon a tanager's nest, held on 5 August 1945 one nestling about a week old and two addled eggs, suggesting that at this

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late date one or both parents were losing their fertility. Usually by late March or early April the dry season is ending and nearly all nestlings are raised when afternoon rains are frequent, wetting the soil and making it easier for parents to find worms and other small terrestrial invertebrates that they bring to their young. At Summit Gardens, on the low continental divide in the Panama Canal Zone, Morton (1971) found 56 nests in which eggs were laid from 26 February to 17 May 1970 (median date 7 April), slightly earlier than in El General, which is at the same latitude but at a considerably higher altitude. At Summit 70 per cent of the nests were active in the dry season, which in this particular year ended around 20 April.

Farther north, where the rains come later, Garden Thrushes breed later. From 19 to 28 June 1937 on "Las Cónavas" coffee plantation near Cartago, at about 1,400 m in Costa Rica's central highlands, I found two nests under construction, three with eggs, and one with nestlings—as many records for June as I have gathered in more than 30 seasons in El General. In late June 1937 the thrushes were singing profusely at Las Cónavas, although they had already fallen silent in El General.

In the Lancetilla Valley, near Tela on the Caribbean coast of Honduras, I found Garden Thrushes nesting freely in May 1930. Nesting appeared to be at its peak in June and July, in each of which I found six active nests. A set of eggs laid on 12, 13, and 14 August was abandoned a week later, apparently because the breeding season was ending. Other late nests that I have seen in northern Central America include one in the lower Motagua Valley of Guatemala with two eggs on 9 July 1932, and one with a newly laid egg near Colomba, around 900 m on the Pacific slope of the same country, on 19 July 1935.

Garden Thrushes frequently lose eggs before completing their set. On three occasions the first egg deposited in a nest promptly vanished and no more eggs were laid in it. I could not learn what the female did with the second egg that must have been ready for laying. When only one of the first two eggs was lost the thrush deposited her third egg in the same nest and incubated only two. After the first egg disappeared from another nest it remained empty for about three days before it received the first of what was apparently a new set of three.

INCUBATION

I have occasionally seen a thrush covering an incomplete set of eggs in the rain. At four nests I have found a thrush sleeping over her first egg before laying her second, or second and third eggs. At two other nests I have found her passing the night on her second egg before laying the third. When I examined a single egg immediately after the bird left it at dawn, it was hardly warm; but the following morning, when she flew from her complete set of two eggs, both were warm. Female birds that sleep over incomplete sets of eggs may not apply their incubation patches closely to them.

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Only the female incubates, as is usual, although not invariable, in the thrush family. One female which I watched through a morning took sessions and recesses, in minutes, as follows (recesses in italics): 20, 82, 28, 84, 22, 34, 11, 36. She covered her three eggs for 74.4 per cent of the morning. Another female, that had already been incubating for 10 days in a nest built upon a bunch of green bananas hanging in a small plantation, divided her time as follows: 58, 10, 53, 14, 29, 11, 40, 13, 188 minutes. Her long session of 3 hours and 8 minutes began at 9:30 and continued until 12:38. She covered her eggs for 86 per cent of the seven hours that I watched—an exceptionally good record.

At neither of these nests was the male attentive. At the first nest he came to the nest tree only once, in the dim light of dawn, and remained beyond view for the remainder of my watch. It was late in the season, 1 July, and all morning I heard him sing only one brief song. At the second nest, on 22 May, the male never once alighted on the banana plant where it was built, but his beautiful song sounded through the plantation during most of my vigil. It was restrained and subdued, not so exuberant as the songs of most Garden Thrushes. The female sat in perfect silence, except that once, when her mate sang from a point nearer the nest than he usually came and she voiced several low, liquid monosyllables before she flew from her eggs to forage. While sitting she at intervals regurgitated seeds that she dropped to the ground.

I wished to watch incubation at the nest which the male had helped to build in front of a window; but the female, which had seemed to ignore people inside the room while she built, became shier after she laid her eggs. No matter how far back in the room I sat, she would not incubate while I watched. Since this was the only side from which the nest was clearly visible, I abandoned the attempt to make systematic observations. But one morning I saw the male, with food in his bill, alight beside the nest voicing low, rattling notes. Instead of taking the food the female flew away. He swallowed what he held and stood looking into the nest for about two minutes. Half an hour later he again came to look into the nest, this time without food. Three days later a nestling hatched.

At seven nests the last egg hatched on the twelfth day after that on which it was laid. At three nests, situated close beside a house where the incubating parent was frequently disturbed, they hatched on the thirteenth day. More precise determinations of the incubation period at three nests were 12 days 6 hours \pm 2 hours, 12 days 7.5 hours \pm 0.5 hour, and 12 days 0.5 hours \pm 4.5 hours. The eggs appear rarely to hatch simultaneously. At one nest all three eggs hatched within about 12 hours, but at three nests the third nestling hatched about 21 to 24 hours after the first. In a nest with four eggs hatching was spread over 40 hours. Empty shells are either eaten at the nest or carried away in the bill, and the same female may use both procedures. One female continued to incubate unhatchable eggs for 17 or 18 days. In the following year a thrush, probably the same

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individual, did so for 19 days, or at least 50 per cent more than the normal incubation period.

NESTLINGS

Feeding and brooding.—While her first nestling hatched in the dawn, a female sat restlessly, higher than usual, and frequently rose up to look beneath herself. Nineteen minutes after carrying away the first piece of shell she brought the first food for the hatchling, a tiny morsel which, after trying vainly for about 30 seconds to make the little one swallow it, she ate herself. Sixty-six minutes after removing the first piece of shell, she succeeded in giving nourishment to the hatchling. In this interval the second egg hatched.

The male thrush came and perched in the nest tree a few feet from the nest, but his mate did nothing to reveal to him what had occurred there. So he flew off, apparently unaware that he was the parent of a nestling, and remained at a distance for two hours and 35 minutes. When next he came the female was absent. Standing upon the nest's rim, he spent about two minutes looking intently down into the bowl, at intervals lowering his head into it and mincingly opening and closing his bill. After this first sight of the nestlings he flew off, and in only three minutes returned with food for them, about three hours after the first one hatched. If his mate had shown him the nestlings when he first visited the nest early in the morning, he undoubtedly would have started to feed them much sooner. The sight of them stimulated him to bring food.

I continued to watch this nest until 10:04. In the first three and three quarters hours after the first egg hatched, the female brooded the nestlings 13 times, for intervals ranging from 1 to 26 minutes and averaging 11.3 minutes. Her 13 absences ranged from 1 to 9 minutes and averaged 3.8 minutes. She covered the nestlings for 74.8 per cent of the time. She brought food eight times and the male brought it six times, often small winged insects or pupae held conspicuously in the tip of the bill. This was more than the hatchlings could take. Unlike some other parent birds, the thrushes did not continue for more than about one minute to offer it to the nestlings. If it was not swallowed in this interval, one parent or the other ate it.

Usually this female left the nest as the male approached, so that he could feed the young directly. Once, however, she remained sitting when he arrived with laden bill. With considerable hesitation he passed to her all but the last item. After swallowing the rest she opened her mouth for this, which he reluctantly gave to her. While she held it in the tip of her bill, evidently intending to pass it to a nestling, he pulled it away from her. Again she opened her mouth to receive it and again he yielded it to her. She held it in her bill as before, and for the second time he snatched it away. This time he swallowed the piece and flew off. Clearly, he was not in the habit of feeding his mate. After feeding the nestlings he sometimes remained

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standing on the nest's rim, guarding it, for as long as five minutes.

At the nest on the bunch of bananas where I had watched the female incubate, the first of three eggs hatched either in the night or in the dim light of dawn on 24 May. When I arrived at daybreak the female had already removed the larger part of the empty shell. At 5:47 she brought the first food and offered it to the hatchling, making a low, clucking sound when the young bird was slow to receive it. Then she settled down to brood, continuing to hold the undelivered food until she flew off with it 25 minutes later. After an absence of 13 minutes, she returned and successfully fed the nestling. In the first seven hours of the day this female fed, or at least offered food to the single nestling that had so far hatched, a total of 18 times, or on each of her returns to brood. Small worms or possibly slugs were the items that she most frequently brought, but they were difficult to identify in her bill. By midday she was offering the tiny nestling such substantial articles as a 2.5 cm-long green caterpillar and a baby lizard about 4 cm long; but much urging, with the usual low, clucking notes, could not induce the newborn young to accomplish what was physically impossible, and the parent finally ate all these larger creatures herself.

During the seven hours this female brooded for 18 intervals, ranging from 2 to 36 minutes and averaging 15 minutes. Her 18 absences varied from 3 to 16 minutes and averaged 8.1 minutes. She covered the nest for 64.9 per cent of the seven hours, which was 21 per cent less than she had spent incubating two days earlier, and 10 per cent less than the other female thrush, whose mate brought food promptly, brooded newly hatched young. Her longest session on the nest, lasting 36 minutes, began at noon. Now the sun, burning through thin clouds, was shining upon her and she half stood over her nestling and eggs, while the second egg hatched beneath her. She ate the empty shell. Unable to swallow the large part whole, she shook it to break off pieces, repeatedly dropping it into the nest and picking it up again.

During a three-hour watch the following morning, the male did not visit this nest on the bananas. He still sang profusely in the plantation, apparently oblivious that the nestlings had hatched. This did not surprise me when I recalled how aloof he had been while his mate incubated three days earlier. Even on 31 May, when these nestlings were a week old, their father had apparently neither seen nor fed them. What a contrast with the male at the first nest, which found and fed his offspring so soon after they hatched!

Development and departure.—Four newly hatched thrushes in two nests weighed 5.7, 5.6, 5.4, and 5.4 g. Their pink skins were lightly shaded by sparse but fairly long, straw-colored down of the usual passerine distribution. Near the end of the upper mandible was a minute egg tooth, and at the tip of the lower mandible was a still smaller projection that apparently also served as an egg tooth, as this lower mandible projected very slightly (less than 1 mm) beyond the upper one. The interior of the mouth was orange-yellow and the flanges at the corners were yellowish. On the roof of the mouth were many inward-pointing bristles, which were longest on

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the rear edge of the cleft palate. The floor of the mouth bore shorter bristles, especially around the opening of the trachea, and longer bristles projected from the posterior margin of the expanded part of the tongue. On the day they hatched the nestlings already peeped and gaped much.

At four days of age the nestlings could open their eyes a little but mostly kept them closed. On this day feather rudiments were visible beneath the skin, and those of the remiges projected slightly. The mandibles were now nearly equal in length. When six days old the nestlings still kept their eyes closed much of the time. At seven days some kept their eyes open and preened their sprouting pinfeathers. When the nestlings were eight days old their feathers began to emerge from the tips of the horny sheaths, except on the head and tail where they were still rudimentary. The most advanced feathers were the primaries, the longest of which already measured 2 cm. A day later the crown feathers and rectrices started to push out of the ends of their short sheaths.

At 12 days of age, the nestlings were nearly covered by their expanding plumage, at least when they sat in the nest with closed wings. At 13 days, when the longest primary measured 5.2 cm, the young thrushes were well feathered and much like their parents, except for the cinnamon-rufous spots at the tips of their wing coverts. The minute egg tooth on the upper mandible was hardly smaller than when they hatched, and the yellowish flanges at the corners of the mouth were still conspicuous. One young thrush tried to escape while being weighed, and jumped from the nest after being replaced. It squawked when I caught it, but was finally persuaded to remain in the nest. Three 13-day-old nestlings weighed 52.7, 53.9, and 60.5 g, the youngest being the heaviest and the oldest the lightest. Although these nestlings remained in the nest two days more, I did not again weigh them. They would not have stayed so long if I had disturbed them again.

These three nestlings slept alone on their last two nights in the nest. At another nest the parent brooded on the nestlings' next-to-last night. An exceptionally attentive parent brooded her single nestling nightly until it left at the age of 16 days. I determined the nestling periods of 27 young thrushes at 15 nests. Four left two nests when 14 days old. Thirteen left ten nests when approximately 15 days old. Ten left six nests on the sixteenth day after they hatched. Occasionally siblings departed their nest at different ages.

Behavior of parents.—Often rather indifferent to a human observer while they build, parent Garden Thrushes become less confident while they incubate and excessively wary as their nestlings approach the age of departure. Wishing to watch two young thrushes leave their nest on a bunch of bananas, I set my blind early in the afternoon beneath a sheltering plantain "tree," about 6 m away. Entering the blind in the following dawn, I watched for two hours, while the parents complained, repeating interminably their plaintive *keyoo* and staccato *tock tock*, and holding food that they would not take to the nest. Meanwhile, the neglected 15-day-old nestlings became very hungry, looked around brightly, and called frequently with a sharp *tsip*.

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Although they were of the age when fledglings usually depart, they did not fly toward their loudly calling parents. Convinced that the adults would not approach the nest while I watched, I took down the blind and left. Next morning the young thrushes abandoned their nest, at the age of 16 days.

No other birds that I know complain so much and so loudly when their nest is, or appears to be, in danger. With angry darts they make squirrels scamper away and threaten hawks much bigger than themselves, often continuing as long as the raptor remains in view, as I saw long ago when a Black Hawk-Eagle (*Spizaetus tyrannus*) carried off the young from a Vermilion-crowned Flycatchers' (*Myiozetetes similis*) nest near their own (Skutch, 1960). Nevertheless, when I have visited nests of Garden Thrushes they have never attacked nor even threatened me, as many a smaller bird has done, but have only complained loudly when I have come near, and sometimes followed me as I walked away, continuing their plaintive cries. I have passed through bushy pastures where many pairs nested, accompanied all the way by the querulous *keyoo* of a sequence of parents, until their cries grated on my nerves. I have never seen a thrush give a distraction display.

Some Garden Thrushes are more querulous than others. In 1961, when a pair raised a single nestling in a crape myrtle tree (*Lagerstroemia speciosa*) close to the house, one of them developed a great antipathy to me, probably because of my occasional visits to their nest, and my frequent activity with a long pole gathering rose-apples and cashews from nearby trees. These thrushes repeated their complaining *key-o-o* all day long, about everything and nothing, until I wondered how such constantly distressed creatures avoided a nervous collapse. The person who took them seriously would have enjoyed no repose. Almost every evening when I went to feed the horse at the front gate, one followed and perched in a tree above me, protesting until his meal was finished. The thrush even cried out when, through an open window, it glimpsed me inside the house, although most of the birds that lived in the dooryard seemed to pay no attention to what went on indoors. One morning while I watched a Silver-throated Tanager (*Tangara icterocephala*) build her nest, sitting about 20 m from the thrush's nest and screened from it by foliage, the thrush perched in the neighboring rose-apple tree and incessantly reiterated its shrill *key-o-o* for over an hour. On the following morning it did the same for an hour.

This thrush evidently remembered me until the following year, when she again nested in the garden. Before I had found her nest, or used my long pole near it, my appearance outside the house, on the side where she nested, set off a series of loud protests. As I walked through the garden she followed me from tree to tree, pausing in each long enough to repeat her remonstrance, then advancing to resume her protests from another, sometimes only 5 m from me. She even followed me up the road on the hillside behind the house; and, as I descended the roadway from a distant excursion, she approached to meet me and protest, then followed me down

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to the house. Since these cries continued while her mate sang, I concluded that the individual which had developed such a strong dislike to me was a female. The area over which she pursued me was about 170 by 120 m, or about 2 ha, from the creek on the east to the crest of the ridge behind the house on the west, and from the forest on the south to the coffee plantation on the north. It was remarkable how often this watchful parent spied me the moment I stepped outdoors.

The appearance of other people of either sex did not disturb this thrush as much as mine did. I was the particular object of her aversion. When I noticed this I decided to test whether she would recognize me despite changes of attire. Just after the bird had complained about me as usual, I entered the house and placed a long, light blue dressing gown over the khaki shirt and dark blue trousers that I habitually wore, while for my khaki cloth hat I substituted a dark blue felt hat. When I went outside in this strange garb, the thrush, which was perching in the cashew tree, called *key-o-o* once or twice, then fell silent. She did not follow me, protesting, as when I wore my usual clothes. A number of other appearances in gown and felt hat failed to elicit a response from the vigilant thrush. Evidently, she recognized me by my whole aspect rather than by my face alone, as birds that have been more intimately associated with humans often do, and as at least some birds recognize one another.

After I had satisfied myself that the thrush failed to recognize me in my disguise, I decided to see how she would react to a sudden change of attire in her presence. In my ordinary clothes I walked out into the garden, the thrush following me vociferously, as usual. Then I donned the gown and hat that I had carried inconspicuously under an arm. After complaining a few times more, the thrush fell silent and ceased to accompany me. Later, while the bird watched, I removed gown and hat, and she immediately resumed her cries.

SECOND BROODS AND REPLACEMENTS

Garden Thrushes frequently re-use old nests, whether they had been successful or had failed. Near sea level in Honduras, two nests from which nestlings had departed, apparently spontaneously, in June were used for second broods in July. In El General, at a higher altitude, my only good evidence for a second brood was provided by the pair that fed a fledgling while together they built a nest in front of a window, as already told.

These thrushes lose so many eggs and nestlings that replacements appear to be much more frequent than true second broods. Twice I have known them to lay again in a nest from which nestlings had been lost. One thrush built upon the remains of the nest from which she had lost a nestling, and two females built and laid in new nests near nests that had failed, in similar sites. Four intervals between the loss of eggs or nestlings and the initiation of a new set ranged from 14 to about 18 days.

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NESTING SUCCESS

Of 61 nests in El General in which at least one egg was laid, 22 produced at least one fledgling, giving a nesting success of 36.1 per cent. These nests were found at all stages, some already with nestlings, thus having already escaped some of the perils to which nests are exposed. Of the foregoing nests, 32 were found not later than the beginning of incubation and, therefore, were exposed to these perils for almost the whole interval that they were occupied, or, if found before the first egg was laid, throughout this interval. Of this smaller sample, 11 nests produced at least one fledgling, giving a nesting success of 34.4 per cent (Table 1).

TABLE 1
Nesting Success of Garden Thrushes in El General

All nests of known outcome	61
Nests successful (at least 1 young fledged)	22
Nests failed completely	39
Per cent of nests successful	36.1
No. of above nests found not later than beginning of incubation	32
Nests successful (at least 1 young fledged)	11
Nests failed completely	21
Per cent of nests successful	34.4
Eggs laid in 32 nests	82
Eggs hatched	37
Per cent of 82 eggs hatched	45.1
Young fledged from 82 eggs	23
Per cent of 82 eggs producing fledglings	28
Per cent of 37 hatchlings fledged	62.1

From 31 nests of the larger sample, eggs or nestlings completely vanished between visits of inspection, having most probably been taken by predators. From one nest a Fiery-billed Araçari (*Pteroglossus frantzii*) carried off the first egg the day it was laid. From another nest one of these middle-sized toucans tore a week-old nestling, the only one that had hatched, in the presence of the protesting parents. Before the big Chestnut-mandibled Toucans (*Ramphastos swainsonii*) vanished from the valley, they probably raided many of the thrushes' nests, as I saw them do at several nests of other kinds. High in a tree that was shedding its foliage and exposing a nest that was originally well screened, one of three Swallow-tailed Kites, (*Elanoides forficatus*), hovering on wing, seized a thrush's nestling but dropped it to the ground when I drove the trio away. Next morning, however, they returned and ate the remaining nestlings. At another nest a large speckled snake devoured two nestlings. Near Cartago in the central highlands I surprised a White-tipped Brown Jay (*Psilorhinus morio*) carrying a fully feathered Garden Thrush, while the parents complained loudly but were unable to save their offspring. These are probably only a few of the predatory birds, mammals, and reptiles that destroy so many of the thrushes' nests.

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Two nests with a total of five eggs were abandoned, probably in consequence of some disturbance. Two nests built on infirm foundations fell, one with three eggs and one with three nestlings. In one nest a newly hatched nestling apparently drowned in a torrential rain, and the survivor was attacked by fire ants (*Solenopsis*). Children gathering fruit knocked down another nest and killed a nestling. Of 109 eggs that were incubated for the full term, 14 in eight nests, including three full sets, failed to hatch. In some I found no trace of an embryo. Thus, 12.8 per cent of the eggs were infertile or otherwise defective—an unusually high proportion.

On 57 ha in parklike Summit Gardens in the Panama Canal Zone, Morton (1971) learned the outcome of 56 nests of which 18, or 32.1 per cent, were successful. Nests in which laying began before the rainy season started, on 20 April 1970, were much more successful than nests in which the first egg was laid after that date. Of 36 nests started in the drier weather, 15 (41.7 per cent) were successful to the extent of producing at least one fledgling, but only 3 of 20 nests (15 per cent) begun after rains became frequent were successful. Morton attributed the greater losses in the wet weather to increased predation and concluded that the thrushes nested early to escape this heavy rain, despite the fact that the rains brought an increase in available food, especially earthworms that contribute much protein for the young. Although more numerous, fledglings from the early nests were lighter than those raised during the rains, and some nestlings died of starvation.

SUMMARY

Among the most familiar birds in Central America, Garden Thrushes sing and nest almost exclusively in dooryards, plantations, shady pastures, and other semi-open areas. After the breeding season they fall silent and spend much time foraging well within woodland, including rain forest.

Much of their food consists of worms, slugs, and other invertebrates gathered from the ground, but they also consume many fruits and arillate seeds. Instead of pecking out pieces, as many birds do, they drop arboreal fruits and seeds too big to force down whole.

The nest is a substantial open cup with an outer layer of coarse materials, including living plants, a middle shell of mud or clay, and a fibrous lining. The heavy structure requires a firm foundation, usually in a tree or shrub, but sometimes in an open shed, on a window sill, or in an open cavity in a tree. Nest sites ranged from 1 to 30 m high, but three quarters of 100 nests were from 1.5 to 3.5 m up. Nests are usually built by the female alone, but one male, which apparently selected the nest site, gave substantial help.

In the Valley of El General most sets of eggs are laid in March, April, and May, with a few belated nests in June and July. In the Panama Canal Zone breeding begins somewhat earlier, and farther north these thrushes sing and nest freely in June and July.

ORANGE-BILLED NIGHTINGALE-THRUSH

The set most often consists of three eggs, frequently two, rarely four. The average size of 115 sets was 2.68 eggs. The pale blue eggs, speckled and mottled with shades of rufous and brown, are laid on consecutive days, often rather late in the morning.

Only the female incubates. Often she spends the night on an incomplete set but appears to apply little heat to the eggs. Her sessions on complete sets often exceed an hour and rarely three hours, and she achieves a constancy of 74 to 86 per cent. The incubation period is most often 12 days but it may be prolonged to 13 days if the female is frequently disturbed. The hatching of a set of three may occur within 12 hours or be spread over as much as 24 hours.

One male first brought food to his nestlings three minutes after he first saw them and three hours after the first nestling hatched, but another male had not yet begun to feed week-old nestlings.

Nestlings are brooded at night until a day or two before they leave the nest, and occasionally as long as they remain there. The nestling period is rarely 14 days, usually 15 days, and frequently 16 days.

Often rather indifferent to a human observer while they build, Garden Thrushes become less confident while they incubate and excessively wary as their nestlings approach the age of departure. They dart with spirit at squirrels and hawks, but when people come near they complain profusely without threatening. A female which developed a great antipathy to the author evidently recognized him by his total aspect rather than by his face, as she was confused when he changed his attire, even in her presence.

Of 61 nests, 36 per cent yielded at least one fledgling. About half the losses were attributable to predation, but 12.8 per cent of 109 eggs that were incubated for the full term failed to hatch because they were infertile or otherwise defective.

ORANGE-BILLED NIGHTINGALE-THRUSH

Catharus aurantirostris

The Orange-billed Nightingale-Thrush, about 15 cm long, has bright brown upper plumage and light gray underparts, becoming white on the abdomen and undertail coverts. Its bill, interior of the mouth, and bare orbital rings are bright orange; the long legs are yellowish orange; and the eyes are brown. The sexes are so similar that in most pairs I could distinguish them only by their bills: the female has a black stripe over nearly the whole length of the culmen, while the male has at most a little black at the base of the culmen. The form that I have chiefly studied has a gray head and was formerly considered a distinct species, the Gray-headed Nightingale-Thrush (*C. griseiceps*), which is confined to the Pacific slope of southern Costa Rica and Chiriquí and Veraguas in Panama, where it has been found on both slopes. Other races of this species, which ranges from Mexico to

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Colombia and Venezuela, have brown heads. Altitudinally, the Orange-billed Nightingale-Thrush is resident from about 400 to at least 1,400 m in Costa Rica and from 400 to 1,700 m in western Panama (Ridgely, 1976). In the southern Andes of Colombia, Wallace (1965) found another gray-headed race (*phaeopleurus*) widespread from 1,500 to 2,000 m or more. In southern Mexico Orange-billed Nightingale-Thrushes with brown heads nest up to about 2,150 m (Rowley, 1962), and in Venezuela other races live even higher, from 800 up to 2,900 m in the Subtropical Zone (de Schauensee and Phelps, 1978).

Although other nightingale-thrushes live in the undergrowth of cool mountain forests of tropical America, the Orange-billed prefers secondary vegetation. Its principal habitats are low, dense thickets, such as in humid regions cover agricultural lands that have lain unsown for several years, and rough pastures where the bushy growth, more than head high, is intersected by a maze of narrow cowpaths. In such tangles it was abundant in 1936 and 1937 around Rivas, at about 900 m in the narrow valley of the Río Buena Vista on the northern side of the Valley of El General, where in two seasons the neighbors' boys and I found 29 nests. In the following nine years, when I studied birds chiefly between 600 and 750 m in El General, I did not meet the nightingale-thrush. About half of this interval was spent at Los Cusingos, which I acquired in 1941. Despite intensive searches for nests of all kinds during four seasons, the first nest of this species was not discovered here until May 1946. Since that date the Orange-billed Nightingale-Thrush has steadily increased at Los Cusingos. Up to 1960 I had found only nine of its nests on the property, but in the last nine years I have found 21.

As it has increased in numbers at Los Cusingos, the nightingale-thrush has occupied more varied habitats, including tall, light second-growth woods, spots in the old forest where gaps in the canopy have permitted a thicker undergrowth, coffee plantations, *milpas* where the maize plants stand twice a man's height, and even the more densely shrubby parts of our garden. Nevertheless, it remains a shy, secretive bird which I have only rarely seen hopping thrushlike, with feet together, over a lawn or close-cropped pasture, hunting food. So difficult is it to follow that I still do not know whether it remains paired throughout the year. The male's persistent singing at all seasons, even during the long interval when the larger thrushes of the genus *Turdus* are silent, suggests that he defends a territory throughout the year.

FOOD

Orange-billed Nightingale-Thrushes are mainly insectivorous, and appear to find most of their food on the ground. Rarely I have seen them rise into a shrub or small tree to gather fruit, including the deep purple berries of *Miconia trinervia* of the melastome family and the seeds, enclosed in red arils rich in oil, of *Clusia*, an epiphytic shrub of the Guttiferae.

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. VOICE

Lacking the liquid sweetness of other species of *Catharus*, the Orange-billed Nightingale-Thrush tirelessly repeats songs that are quaint or whimsical rather than melodious. Often they consist of three or four syllables, which I have variously paraphrased as *thanks very much*, *that's very nice*, or *Will Shakespeare*. Even while singing the nightingale-thrush avoids high, exposed perches but proclaims his presence amid low tangles, where he remains unseen. At all seasons he is among the very first birds to sing in the dim light of dawn, and the last to become silent as twilight fades into night. Rarely an Orange-bill ends his short song with a slight trill. One sang *che-what ch-r-r-r*. These birds call, and complain when their nest is disturbed, with a nasal or mewling *chaaa* much like that of the Gray Catbird (*Dumetella carolinensis*). Another note, less frequently heard, and apparently also an expression of displeasure or anxiety, is a prolonged, thin whistle, *kreee* or *tseee*. The songs and calls of the brown-headed race (*costaricensis*), as I have heard them in the central highlands of Costa Rica, are quite similar to those of the gray-headed race.

NEST

In the Valley of El General some Orange-billed Nightingale-Thrushes start to build around the middle of March, but nesting is not widespread until April. Most of the nests that I have seen were situated amid thickets difficult to penetrate, although often they were in more open spots amid the untidy growth, or beside a cowpath. Less often they were in tall, light second-growth woods, where the undergrowth was more open than in thickets unshaded by higher trees. A few were in fields overgrown with low weeds. Three were beside the shady banks of streams. Since these thrushes have become more abundant, I have found more of their nests in cultivated plants. Five were in coffee shrubs, four in young orange or grapefruit trees, six in tall maize plants and one on a stump in the midst of a *milpa*, one on a sugarcane, and two in privet hedges. In three consecutive years, an Orange-bill built above the growing point of the same tree fern standing at the edge of open pasture. None of these nests was more than a short flight from a thicket or the dense vegetation at the forest's edge. One nest was on a spiny palm in second-growth woods. The lowest nest that I have seen was only 9 cm above the ground; the highest, 3 m. Most were from 90 cm to 2.1 m up. The heights of 63 nests were as follows:

Under 30 cm:	1 nest
30 cm to 90 cm:	6 nests
90 cm to 1.5 m	28 nests
1.5 m to 2.1 m	19 nests
2.1 m to 2.7 m	6 nests
2.7 m to 3.0 m	3 nests
Total	63 nests

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Through most of their great range, Orange-billed Nightingale-Thrushes build their nests at about the same heights. Eight nests in southern Colombia were from 60 cm to 2 m up (average 113 cm) (Wallace, 1965). In Morelos, Mexico, five nests in thorn thickets were from 1.2 to 1.8 m high, but two in pine-oak woodland were 3.7 and 4.5 m above the ground (Rowley, 1962).

At the single nest of which I watched the construction, only the female built. In two hours of the early morning she brought material 17 times, coming each time with her bill laden with many pieces that probably took several minutes to collect. After depositing her load in the half-finished cup, she sat in it to shape it with her whole body. While she worked her mate sang much of the time in the neighboring thicket. Although he did not follow her back and forth as she brought contributions to her nest, he came at intervals to perch on the rim and inspect it. Once he sang while he stood there.

The completed nest is a bulky, thick-walled, open cup. The wall is composed of coarse herbaceous stems, straws, and grass blades, and often enough moss to make the nest green. The interior is well lined with rootlets, fine tendrils, dry inflorescences, fine secondary rachises of mimosa leaves, and vegetable fibers. A typical nest is 12 cm in diameter by 9 cm high. The cavity is 6 cm in diameter by 5 cm deep.

EGGS

With a single possible exception, each of 61 nests of the Orange-billed Nightingale-Thrush that I have recorded in El General contained two eggs or nestlings. The first egg of a set is laid rather late in the morning; the second either in the afternoon of the next day or in the morning of the second following day. At one nest the first egg was laid between 7:15 and 9:40 on 16 June; the second between 12:00 and 13:55 on 17 June. At another nest the first egg was laid after 8:30 on 27 May; the second egg in the afternoon of the following day. At a third nest the first egg was laid between 7:00 and 13:00 on 1 May; the second before 8:40 on 3 May. The eggs are blue or pale blue, speckled and blotched all over, but most heavily on the thicker end, with brown, rufous-brown, cinnamon, or pale lilac. The measurements of 25 eggs average 23.7 by 17.5 mm. Those showing the four extremes measured 26.2 by 17.9, 25.0 by 18.3, 21.8 by 17.5, and 24.2 by 16.7 mm.

In 61 nests in the Valley of El General, 750 to 900 m above sea level, from 1936 to 1979, eggs were laid as follows: March, 3; April, 20; May, 18; June, 10; July, 7; August, 3. At Rivas, around 900 m, in 1936 and 1937, 14 of the foregoing sets of eggs were laid in April and only 4 in May. At Los Cusingos, about 150 m lower and 16 km distant, from 1946 to 1979, only 6 sets were laid in April and 14 in May. It appears that at higher altitudes the nightingale-thrush starts to nest earlier. However, my earliest dates for laying are 30 March 1937 at Rivas and 27 March 1959 at Los Cusingos. At Popayán in southern Colombia, laying began about 15 March (Wallace, 1965).

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Although I have never seen more than two eggs in a nest of *C. aurantirostris griseiceps*, a nest of *C. a. costaricensis* that I found near Cartago, Costa Rica, at about 1,400 m above sea level, contained three feathered nestlings on 1 July 1952. However, another nest, situated amid dense shrubbery in the same garden on 29 April 1951, and two discovered by Cherrie (1891) in the central highlands, each held only two eggs. In situation and construction the nests of the brown-headed race closely resembled those of the gray-headed race, but the eggs were rather different. Cherrie recorded their ground color as "pea green," whereas those that I found were pale gray, finely sprinkled with bright cinnamon-rufous, which on the thicker end nearly concealed the ground color. In Cauca, Colombia, 2°26' north of the Equator, Orange-billed Nightingale-Thrushes lay two eggs, as they do in Costa Rica, but much farther north in Morelos, Mexico, at 18°N, each of seven nests held a set of three—another example that the latitude effect is manifest even within the tropics (Wallace, 1965; Rowley, 1962).

INCUBATION

Only the female incubates. I have repeatedly found her sitting on the first egg before she laid the second. Table 2 summarizes records of incu-

TABLE 2
Incubation and Brooding by Female Orange-billed Nightingale-Thrush¹

Nest no.	Hours watched	Sessions in minutes			Recesses in minutes			Constancy %
		No.	Range	Average	No.	Range	Average	
20	11	26	5-56	12.6	25	5-24	13.2	48.8
28	5	9	7-32	17.2	9	11-19	15.1	53.3
31	6	10	11-39	25.6	10	8-19	11.9	68.3
50	7	9	14-66	35.0	9	7-17	11.9	74.6
51(1)	7.5	7	14-80+	49.7	6	10-28	17.8	73.6
51(2)	6	8	4-52	29.4	8	8-21	13.9	67.9
51(3)	4	14	1-35	11.1	13	2-12	6.8	63.9
55(1)	7	4	7-277	87.5	4	6-38	17.5	83.3
55(2)	3	6	5-30	16.7	6	7-22+	13.7	54.9
25	4	4	34-59	47.5	4	2-13	73.0	86.7
63	3.75	3	15-124	56.3	3	12-23	18.7	75.1

- Nest 20. 5:30-11:30 on twelfth day of incubation, 13:00-18:20 on thirteenth day
Nest 28. 5:45-10:47 on ninth day of incubation
Nest 31. 5:50-11:49 on ninth day of incubation
Nest 50. 5:05-12:19 on eighth day of incubation
Nest 51(1). 5:09-12:45 on thirteenth day of incubation
Nest 51(2). 4:54-10:54 on pipped eggs
Nest 51(3). 6:30-10:43, with nestlings less than 1 day old, both parents feeding them
Nest 55(1). 5:05-12:05; both eggs hatched about 10:30; male did not attend
Nest 55(2). 6:50-10:00, with day-old nestlings; male not yet feeding
Nest 25. 6:10-10:10; one nestling hatched about 6:30, when both parents were already bringing food.
Nest 63. 8:55-12:40; first nestling hatched at 8:50; male started to feed at 9:14

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bation at six nests watched for a total of 42.5 hours. Of the five female nightingale-thrushes, the first, at nest 20, was the least constant in attendance on her eggs, covering them for slightly less than half of the 11 hours that I watched. With the exception of a session of 56 minutes during a light shower in late afternoon, her longest interval on the nest was only 21 minutes—less than the longer sessions of the other four females. The average length of her sessions was much shorter than that of any of the others. I attribute her poor record to the fact that, of the five females, she had by far the most attentive mate. He was readily distinguished by his song, which she seemed to lack, and by his bill, which was almost wholly bright orange, whereas hers had a black stripe along the culmen, broadening toward the base. He consistently alternated with her in attendance at the nest, guarding, but never incubating, while she was absent.

The male's behavior was the more striking because, while the female incubated, he rarely remained for many minutes near the nest. As he arrived, singing, she usually flew from her eggs. Although sometimes she left before I was aware of his approach, she probably heard or saw him, for almost always he appeared soon after her departure. If she did not leave within a few minutes of his arrival, he wandered off again; but seldom did he leave the nest unguarded while she was absent. He had no special perch from which to watch the nest but moved about among the surrounding bushes, usually within two or three meters of it. Most of the time he rested low in the tangled vegetation at the foot of the bank above which the nest was situated, where he could not see what the nest contained; but from time to time, while his mate was away, he came to stand on the rim and attentively examine the eggs. While guarding the nest he tirelessly repeated his simple but pleasant song. Only in the warmest midday hours did his singing wane, but during no watch was he wholly silent. When I approached the nest, on days when I was not making a record of incubation, he flitted around a few meters from me and protested with loud, nasal news, without ever daring to attack. After his mate returned to her eggs, he usually wandered beyond view, and often also beyond hearing.

This female nightingale-thrush was very sensitive to heat. During the warmer hours of the day she sat much with open mouth, panting, even when not in sunshine. The tropical species of *Catharus* are mostly inhabitants of cool mountain forests. Intolerance of heat may limit the downward distribution of this and other members of the genus.

At Nest 28, where the female sat with slightly greater constancy than at Nest 20, the male failed to guard during the five hours of my watch. Although he sang much, he was mostly beyond sight. I detected no relation between his singing and the female's movements. At Nest 31 four of the female's 10 departures occurred when her mate approached the nest, singing, after an interval when he was more distant. At Nest 50 the singing male's approach appeared to be the signal for eight of the female's 10 departures; and at Nest 51(1) the male's songful approach concided with all five of his mate's spontaneous departures. But none of these males alternated with

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his mate as consistently as the first did. Their guarding was sporadic and undependable. However, the male of Nest 51 chased away a female Song Tanager (*Ramphocelus passerinii*) and, later, a male White-winged Becard (*Pachyramphus polychopterus*). Both the male and the female nightingale-thrushes ignored two tiny male Tropical Gnatcatchers (*Polioptila plumbea*) that alighted on the tree fern that bore the nest.

As at Nest 20, so at Nests 31, 50, and 51 the males from time to time alighted on the rims to examine the contents; but none so often as the first male, who made 10 visits of inspection in the morning and two more in the afternoon. Each of the others inspected his nest only thrice in a morning. Once at Nest 50, and twice at Nest 31, the male came to the nest holding in his bill a particle of food that he promptly swallowed. These were evidently instances of anticipatory food bringing. But none of these males tried so earnestly to deliver the food to the eggs as I have seen at nests of certain other species, and none fed his mate. Strangely, while the female incubated pipped eggs in Nest 51(2), her mate did not once inspect them during six hours, although he often sang nearby; and at Nest 55(1) the male did not look into the nest on the morning that the eggs hatched. Nests 51, 53, and 55 were in the same tree fern in 1974, 1975, and 1976.

While I sat in my blind amid a thicket, on 1 May 1936, watching a Bran-colored Flycatcher's (*Myiophobus fasciatus*) nest, I also had in view a low nest of the Orange-billed Nightingale-Thrush with two newly laid eggs. During one of the nightingale-thrush's absences, a Slaty Castlebuilder (*Synallaxis brachyura*), foraging through the thicket, happened to find her nest. Alighting on the rim, the wren-sized bird looked attentively into the nest, then struck the nearer egg with its sharp, black bill, piercing the shell. Then it continued its course through the thicket, without eating any of the egg it had broken or harming the other. Its motive in pecking the egg may have been curiosity. When the nightingale-thrush returned she promptly noticed that an egg had been damaged, but she appeared not to be upset. For several minutes she continued to lower her head into the nest and raise it again, mincingly opening and closing her bill, as though drinking. Evidently she was sampling her egg and finding it palatable. Finally, she snuggled down in her nest to warm the broken egg along with the sound one. After sitting for nearly 20 minutes she rose up, tasted the egg a few times more, then grasped it with her lower mandible in the hole and carried it beyond view. In three minutes she returned, alighted on the nest's rim, pecked at the spot where the broken egg had lain, and moved her mandibles mincingly as before. Then she jumped into the nest to incubate her remaining egg.

While incubating pipped eggs, the female at Nest 51(2) (Table 2) sat with about normal constancy. But two years later the female at Nest 55(1), in exactly the same site, sat continuously for the exceptionally long interval of four hours and 37 minutes (277 minutes) while her eggs hatched beneath her. She sat almost motionless the whole time, not fidgeting nor rising

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up to look beneath herself, as some birds do while their eggs hatch. Meanwhile her mate sang in the distance but remained aloof from the nest. Her behavior contrasted with that of a female nightingale-thrush that I watched many years earlier while her eggs hatched. For seven minutes she rested on the nest's rim, much of the time keeping her head down in the bowl where I could not see what she did. Possibly she assisted the hatchling to escape from the shell.

About 18 to 21 hours after the first detectable fracture of the shell the eggs hatch. At two nests the empty shells were carried away rather than eaten by the female parent—as happened at a nest watched by Wallace (1965) in Colombia. At another nest the male carried away the large part of the shell about two hours after the hatchling emerged from it. Nearly an hour later the female removed the smaller piece of the shell. At three nests the incubation period was approximately 13 days; at five it was 14 days; at three it was 15 days; and at one it was 16 days. My most accurate determination gave an incubation period of 14 days 1 hour \pm 4 hours, which is close to the average of the foregoing 12 periods. At a nest in Colombia the incubation period was a few hours more than 14 days. The incubation period of the Orange-billed Nightingale-Thrush is about two full days longer than that of the much bigger Garden Thrush—just as, among tanagers, flycatchers, and other birds, the eggs of smaller species often take substantially longer to hatch than those of larger species. At one nest of the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*), high in the mountains, the incubation period was 15 days, and at another it was 15 or 16 days.

NESTLINGS

In my earlier account of the Orange-billed Nightingale-Thrush (1960), I told in detail how, at the nest where the female stood on the rim watching an egg hatch, both parents brought food before the hatchling could take it, probably before it had escaped from the shell. For intervals up to five minutes they patiently coaxed the hatchling to swallow the tiny insects that they offered, sometimes without success. Accordingly, the mother ate some of the food that she brought for her little one, and most of that which her mate brought to the nest. He brought so much—nine times in one hour—that the female carried some of the items away. With such substantial support from her partner, the female was able to warm the nestling almost continuously during its critical first hours out of the shell, achieving the highest constancy of sitting that I have recorded for this species (Table 2, Nest 25). During her absences the male stood on the nest's rim, guarding the nestling, once for as long as 13 minutes.

At Nest 63, where the first egg hatched at 8:50, the male came 24 minutes later with a tiny green caterpillar which he presented to his mate. For two minutes she tried to give it to the hatchling, then ate it herself. The male gave the hatchling its first small meal at 11:19, its second at 11:35.

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By 13:00, more than four hours after its emergence from the shell, the hatchling had received only these two meals from its father, but nothing that I could detect from its mother. Standing on the rim both parents repeatedly poked down into the nest, peered in with one of both eyes, and made mincing movements with their mandibles.

At Nest 51, where both eggs hatched on a rainy afternoon, the male was feeding the nestlings early on the following morning, and possibly sooner. Two years later, in the identical site at the top of a tree fern, an egg hatched about 10:00 on 23 May but the male failed to visit the nest from 6:50 to 10:00 on 24 May (Table 2, Nest 55(2)). At 6:51 on 25 May I watched him alight on the nest with food in his bill, only to leave immediately without having delivered it. Once more he alighted near the nest, only to leave without feeding. At 6:54 he fed a nestling, evidently for the first time. Thus, in strong contrast to the males of Nests 25 and 63, this male apparently delayed nearly two days, and certainly one full day, to begin feeding his offspring. These contrasts, like those noticed during the incubation period, reveal some of the great individual differences in behavior that can arise within the same general pattern of nest attendance.

The female, in closer contact with the nest, does not delay so long to feed the hatchlings as her mate sometimes does. As we have seen, one female offered a hatchling food as it was emerging from the shell. Another (Nest 55) first brought food 52 minutes after the conclusion of the session during which her first nestling hatched. Very soon after escaping from the shell, before they have dried, the nestlings lift up their gaping mouths, exposing a bright yellow interior with pale yellow flanges at the corners. Details of brooding newly hatched young are given in Table 2.

After the male begins to feed he does so diligently. In 4-1/4 hours of the morning two nestlings that had hatched in the preceding afternoon were fed 12 times by their father and 13 times by their mother, or at the rate of 3 times per nestling per hour. The female also spent much of this period brooding (Table 2, Nest 51(3)). When the male found his partner sitting, he passed the food to her for delivery to the nestlings. In her absence he fed them directly. Both parents brought small, unidentifiable items in their bills and delivered the food rapidly, without coaxing the nestlings to take it. Droppings were apparently all swallowed, as I saw none carried away in the parents' bills. The male sang less than while his mate incubated.

When the two nestlings in Nest 20, where the male was so extraordinarily attentive, were two and three days old, I watched them during the first two hours of the day. Their father brought food 11 times, their mother 4 times, in addition to brooding for 50 of the 120 minutes. The few articles that she brought were larger than the male's contributions. It did not take him long to find food. When on one of his visits of inspection the young hungrily stretched up their gaping mouths, he immediately flew off to seek something for them, and in a minute he returned with an insect. Once, after feeding a nestling, he delayed for five minutes on the rim, picking

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off minute objects that were probably ants. He drove away a Rufous-breasted Wren (*Thryothorus rutilus*) that came to hunt insects in the bushes 2 m from the nest.

When the young in Nest 51 were 12 days old and well feathered, I watched for five hours of the morning, during which they were fed 53 times, or at the rate of 5.3 times per nestling per hour. The number of meals delivered in single hours varied from 13 meals between 7:00 and 8:00, and also in the following hour, to 7 meals between 10:00 and 11:00. Often the meal was delivered so quickly that I could identify neither the feeder nor the food. The male appeared to bring more than the female: I credited him with 23 feedings and her with 15, but admit the possibility of error. Usually the parent came with a single item held conspicuously in its bill, rarely with two. With a single exception all the food that I saw clearly was animal. Most often I noticed caterpillars or other larvae, whose whitish or dark, rarely green, color suggested that most had been collected on the ground rather than amid foliage. One item appeared to be an earthworm. I recognized only three winged insects, one green, one rather large of an undetermined kind, and one apparently a medium-sized moth. The single fruit was bright red and appeared to be a raspberry from the garden. On each parental visit a single nestling was fed, very swiftly. Both parents carried away droppings in their bills. Except when another nightingale-thrush sang not far off, the male parent sang little. Sometimes he sang in an undertone while bringing food. The parents were now more tolerant of other small birds. Several times a female Song Tanager clung to the trunk of the tree fern that held the nest, without being threatened.

Hatched with long but sparse gray down that fails to conceal their pink skins, the nestlings are well feathered when 10 or 11 days old. Twenty-two nestlings departed 12 nests, all apparently spontaneously, at ages ranging from 12 to 17 days. Two left at 12 days, one at 13 days, ten at 14 days, four at 14 or 15 days, three at 15 days, and two at 17 days. My most accurate determination of the nestling period was 14 days 2 hours \pm 3 hours, for two siblings. The two nestlings that remained in the nest for 17 days hatched after only 13 days of incubation, whereas the two that left when only 12 days old took 16 days to hatch—facts which suggest that a nestling's development takes longer if it hatches prematurely, but the nestling period may be shortened if the incubation period is prolonged.

Some 14-day-old fledglings fly strongly, at times as much as 30 m before alighting. They have dark olive-brown dorsal plumage and mottled gray breasts. Their bills are dusky with light tips and persisting, pale yellow, oral flanges. The interior of the mouth is yellow. Their eyes and orbital rings are dark, and their legs and toes are yellow. After quitting the nest the young promptly vanish into dense thickets where their parents lurk, so that it is hardly possible to follow their subsequent history in the wild. Wallace (1965) raised a juvenile of the Colombian race to the age of about three and a half months and found him "tame, playful, and sociable." He gives interesting details of the young nightingale-thrush's development.

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NESTING SUCCESS

I lack information on second broods and replacement nests. The nests that I have followed have enjoyed greater success than those of other birds in the same locality. Of 27 nests found at all stages, 17, or 63 per cent, produced at least one fledgling (Table 3). One nest was invaded by fire ants, causing the nestlings to leave when only 10 days old, and probably to perish. In one egg the embryo died at an early stage. For all the other losses undetected predators were apparently responsible. Nestlings are sometimes parasitized by *tórsalos*—dipterous larvae that cause prominent swellings beneath the skin. The development of these parasites is rapid; in a few days they vanish, without detectable injury to their hosts.

TABLE 3
Nesting Success of the Orange-billed Nightingale-Thrush

All nests of known outcome	27
Nests successful (at least 1 young fledged)	17
Nests failed completely	10
Per cent of nests successful	63
No. of above nests found before incubation	14
Nests successful (at least 1 young fledged)	9
Nests failed completely	5
Per cent of nests successful	64.3
Eggs laid in 14 nests	27
Eggs hatched	19
Per cent of 27 eggs hatched	70.4
Young fledged from 27 eggs	17
Per cent of 27 eggs producing fledglings	62.9
Per cent of 19 hatchlings fledged	89.5

SUMMARY

The Orange-billed Nightingale-Thrush inhabits low, dense thickets, coffee plantations, maize fields, and forest openings choked with tangled vegetation. It forages chiefly on the ground and supplements its largely insectivorous diet with berries and arillate seeds.

Throughout the year males repeat their quaint songs, which consist of short phrases with little melody.

The female builds the nest, a substantial, usually moss-covered, open cup. The site is a thicket, light secondary woods, a coffee plantation, a maize plant, a citrus tree, or a hedge, rarely far from a sheltering thicket. The heights of 63 nests ranged from 9 cm to 3 m. Most were 90 cm to 2.1 m up.

Sixty nests of the race *griseiceps* contained two eggs or nestlings; none more. The first egg of a set is laid rather late in the morning, the second either in the afternoon of the next day or the morning of the second following day. One of four nests of the race *costaricensis* had a set of three.

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In the Valley of El General laying continues from March to August, but most sets are laid in April and May. Nightingale-thrushes bred earlier at 900 m than they did 150 m lower.

Only the female incubates, with a constancy ranging from about 50 to 75 per cent. The female with the lowest constancy had the most attentive mate, whose arrival was the signal for her departure from the nest.

Some males guard the nest during the female's recesses. Most come from time to time to inspect the eggs, sometimes bringing food—anticipating the nestlings. They have not been seen to give food to their mates before the young hatch.

During the time when eggs were hatching beneath them, some females took extraordinarily long sessions, up to 4.5 hours.

At 12 nests the incubation period varied from 13 to 16 days, but most eggs hatched in 14 or 15 days. Shells are carried away by either parent.

Both parents feed the young, chiefly with larval insects that appear to be gathered from the ground. At one nest the male had food for the first nestling as soon as it hatched, and was soon bringing more than it and its brooding mother could eat. Other males have started to feed less promptly; one did not begin until the nestlings were more than 24 hours old. Feathered nestlings were fed at the rate of 5.3 times per hour for each of them.

Twenty-two nestlings left the nest at ages ranging from 12 to 17 days, most of them at 14 days, when they flew well.

Of 27 nests, 63 per cent were successful. Nightingale-thrushes enjoyed greater success than other birds in the same locality.



FIG. 10. Green Honeycreeper, *Chlorophanes spiza*, and Golden-masked Tanager, *Tangara larvata* (above).

Family COEREBIDAE
GREEN HONEYCREEPER

Chlorophanes spiza

Despite the devastating deforestation along the Pacific slope of southern Costa Rica in the last few decades, the widespread Green Honeycreeper remains abundant, as it thrives in clearings with scattered trees as well as in the upper levels of rain forest. Although in my earlier account (Skutch, 1962) I recorded its altitudinal range as extending from near sea level up to 900 m in this region, actually it occurs higher than this, as from March to June it was abundant at nearly 1,200 m in the foothills of the Cordillera de Talamanca near the Panamanian border. In Venezuela it ranges upward to 1,400 m at the lower edge of the Subtropical Zone (Phelps and Phelps, 1963). An unsociable bird that does not join in flocks of its own kind, it is, nevertheless, often found with other honeycreepers, tanagers, finches, and other birds at generously fruiting trees.

FOOD

The Green Honeycreeper's diet is varied, consisting of liberal quantities of fruits, arillate seeds, nectar, and insects. It is readily attracted to feeders where bananas, plantains, and halved oranges are offered. I have had a male peck at a banana held in my hand. Of wild fruits it eats the small berries of species of *Miconia* and other trees and shrubs of the melastome family, the larger berries of the solanaceous epiphytic shrub *Lycianthes synanthera*, and the green fruiting spikes of *Cecropia* trees. Above all, it seeks arils rich in oil, including those of the trees *Alchornea costaricensis* (Euphorbiaceae), *Casearia sylvestris* (Flacourtiaceae), *Dipterodendron elegans* (Sapindaceae), *Protium* sp. (Burseraceae), epiphytic trees and shrubs of *Clusia* spp. (Guttiferae), and the epiphytic vine *Souroubea guianensis* (Marcgraviaceae). Green Honeycreepers peck fragments from the large white arils of *Dipterodendron* and *Protium* and, accordingly, fail to disseminate the seeds, as is done by larger birds that swallow them whole. At opening pods of *Casearia*, *Clusia*, and *Souroubea*, they eat the massed red or orange arils along with the small seeds embedded in them. At a tree of the large-fruited *Clusia rosea*, where competition for the red arils was keen, Green Honeycreepers displaced Blue (*Cyanerpes cyaneus*) and Shining (*C. lucidus*) Honeycreepers from slowly opening pods, but were in turn displaced by Golden-naped (*Melanerpes chrysauen*) and Red-crowned (*Melanerpes rubricapillus*) Woodpeckers (Skutch, 1972).

In my earlier account (1962), I told how Green Honeycreepers were attracted by a flowering vine of *Marcgravia* that grew over a tall forest tree in the Pacific lowlands near the Golfo Dulce. Four or five of these honeycreepers were sometimes present together, sipping nectar from the cuplike nectaries clustered beneath pendent whorls of green flowers, catching

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insects attracted to them or, more probably, taking advantage of both sources of nourishment—the birds were too high for me to distinguish details. I have also watched Green Honeycreepers, in company with Blue Honeycreepers, Turquoise Dacnises (*Dacnis cayana*), and Bananaquits (*Coereba flaveola*), extracting nectar from the flowers of tall, spreading shrubs of *Calliandra similis* (Leguminosae, Mimoseae) in a riverside thicket. All these small honeycreepers perched on supporting twigs just inward from the flowers, and bent down to thrust their slender bills deep into the clusters of long, red stamens. All fed amicably except the Green Honey-creeper which, after satisfying his appetite, continued to dart at the other birds, trying to chase them away.

From July to September when tall trees of *Symphonia globulifera* (Guttiferae) growing in the forest are profusely laden with flowers that resemble clustered red cherries, Green Honeycreepers frequently probe them, doubtless for nectar, along with Brown Violet-ears (*Colibri delphinae*), Jacobin Hummingbirds (*Florisuga mellivora*), Shining Honeycreepers, Blue Honeycreepers, Bananaquits, and occasional avian visitors of other kinds. When the rose-apple tree (*Eugenia Jambos*, Myrtaceae) beside our house flowers, Green Honeycreepers spend much time sipping nectar from amid the spreading clusters of long, white stamens. They also take nectar from the small white flowers of *Croton glabellus* (Euphorbiaceae) and *Serjania mexicana* (Sapindaceae).

On the island of Trinidad widespread Green Honeycreepers take much the same foods as in Costa Rica. Of 267 records of foraging gathered by Snow and Snow (1971) 15 per cent were of insect-searching, 63 per cent of fruit-eating, and 22 per cent of flower-visiting. Slightly more than half of the insect-searching was at flower and seed heads. Twenty per cent was aerial flycatching. Fruits and arillate seeds eaten by Green Honeycreepers included *Clusia* spp., *Protium heptaphyllum*, *Miconia* (8 spp.), *Didymopanax morototoni* (Araliaceae), *Chiococca alba* (Rubiaceae), *Alchornea glandulosa*, *Hieronyma caribaea*, *Sapium aucuparium* (the last three Euphorbiaceae), *Trema micrantha* (Ulmaceae), *Cecropia peltata*, *Ficus* spp. (both Moraceae), and mistletoes (Loranthaceae).

BEHAVIOR AND VOICE

Not long ago I watched a female Blue Honeycreeper shaking and preening dripping feathers in a guava tree behind our house. After she left a female Green Honeycreeper came to bathe in the rain water that had collected in a cavity, made by decay, in the cut-off end of a thick ascending branch. Repeatedly the green bird immersed herself in this little aerial pool, then stood on the rim to arrange her soaked plumage. My wife watched a Green Honeycreeper bathe in a tank bromeliad. At least three times I have seen a Green Honeycreeper engage in the curious, perplexing activity known as "anting," always in a tree. Although birds in the temperate zones usually ant on the ground, all that I have seen so engaged in tropical America, not excluding such largely terrestrial birds as the Buff-rumped Warbler

GREEN HONEYCREEPER

(*Basileuterus fulvicauda*) and Black-striped Sparrow (*Arremonops conirostris*), were in trees (Skutch, 1977).

I have never heard a Green Honeycreeper sing. Its usual note is a sharp, wood warblerlike *chip*, which is often heard when a number of honeycreepers are gathered around a source of food, and appears to be an expression of annoyance. When more seriously perturbed the Green Honeycreeper produces a low, dry rattle, which I have often heard when the honeycreeper joins a mixed crowd of other small birds mobbing a snake, or complaining about a big, bedraggled moth that has attracted a number of temperamental Scarlet-rumped Tanagers (*Ramphocelus passerinii*), whose excited cries drew a varied crowd of feathered onlookers. One of the few owls that I have seen in this valley was a somnolent Spectacled Owl (*Pulsatrix perspicillata*) that rested by day high on a slender branch in the forest, with its great head and massive body made more impressive by its puffed-out plumage. It seemed huge in comparison with the smaller birds that had gathered around to inspect it or protest its presence. These included several hummingbirds and trogons, and a male Green Honeycreeper that approached closer to the impassive owl than the trogons did, but not so near as the tiny hummingbirds.

Sometimes a Green Honeycreeper undertakes alone to mob a potentially dangerous bird or snake. On a morning in June a Double-toothed Kite (*Harpagus bidentatus*) sat, conspicuous against the sky, at the top of a tall dead tree at the forest's edge, while it leisurely preened. About a meter behind the raptor, on another slender dead branch, perched a male Green Honeycreeper, facing the much bigger kite. For the next 25 minutes the green bird remained there, always with its bill toward the preening kite. That the honeycreeper stayed to watch the kite was evident from his growing restlessness: he fidgeted from side to side, stretched his wings, sometimes preened a little. Finally, his patience exhausted, he flew away leaving the phlegmatic kite in the same spot, where I found it an hour later. Although the Double-toothed Kite is mainly an insect-eater (Skutch, 1965) it is not above robbing an occasional bird's nest or catching a small bird.

One cloudy afternoon in June the constantly reiterated low, sharp rattle of a Green Honeycreeper in a spreading mango tree beside my study, caused me to drop my writing and go out to investigate. After much peering up into the dense cluster of leaves toward which the bird's scolding was directed, I detected part of the shiny green body of a tree snake, resting well above my head. To protect the birds nesting in the garden, I remove intruding snakes, so I went for my rifle and shot twice at this one. The serpent did not budge. Then I took a long pole and shook the branch where it rested. Still no response! Further investigation showed that the supposed snake was only a longitudinally curled green leaf, wet and shiny from the recent rain! Evidently the honeycreeper, which had a much closer view than I did, mistook it for a snake, and I was misled by him. Birds not infrequently mistake their own reflection in a window or other reflecting surface for another individual, but this was the only time I have known

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a bird to be deceived by a leaf or vine that resembled a snake.

My earlier account told of a male Green Honeycreeper that seized an immature Plain-colored Tanager's (*Tangara inornata*) leg and hung from it, while the tanager clung to a twig with its other leg, until I chased the attacker away. While a variety of honey-creepers were competing for the arillate seeds of a *Clusia* tree, a male Green Honeycreeper seized a wing tip of a Blue Honeycreeper, which dangled below the assailant with both wings stretched out. More frequently I have seen a male Green Honeycreeper firmly grasp the tail of a female of his kind and hang tenaciously while she tried hard to pull away, sometimes crying out in pain or alarm. At times the female so assailed is the attacker's building mate. One afternoon in February the rapid repetition of sharp notes drew my attention to a guava tree close by the board where the birds ate bananas. A male Green Honeycreeper was holding the tail of a protesting female Green Honeycreeper, which tried hard to break away. A second male was nearby. When finally the female escaped, she was closely pursued by three males in full adult plumage. Apparently, male Green Honeycreepers try to obtain mates by seizure in the manner of males of certain human tribes. I have never seen a female Green Honeycreeper, or any bird of other species, behave in this fashion. The only other example of tail-pulling that has come to my attention is of a very different bird, the Shag (*Phalacrocorax aristotelis*). These cormorants pull each other's tails somewhat as Green Honeycreepers do, perhaps to get attention (B. K. Snow, 1963).

In a family of gentle, pacific birds which usually settle their differences by nonviolent calling and posturing, the rude, sometimes ruffianly Green Honeycreeper is exceptional. Nevertheless, he is capable of gentler behavior and often, instead of pulling a female's tail, resorts to more usual modes of courtship and offers her a gift. I have witnessed this repeatedly, but never more clearly than on a morning in May, while I watched a pair eat the abundant berries of a small melastomaceous tree beside a pasture. The male plucked a berry and offered it to his mate, which promptly swallowed it. Then they flew off together. As we shall see, the male Green Honeycreeper also feeds his mate while she incubates.

NESTING

Although on the exceptionally early date of 17 March 1972 I watched a Green Honeycreeper build a nest that was apparently never used, nesting usually does not begin in the Valley of El General until the second half of April. The 11 nests that I have seen, under construction or completed, were in trees, shrubs, or bamboo sprays at the forest's edge, or in a garden or pasture a short flight from woodland. In height these nests ranged from 1.5 m to about 12 m, with six at 6 m or more and only two below 3 m. The slight structure is usually well hidden by foliage clustering around it, and sometimes also by an epiphytic orchid or fern.

At two nests that I watched for more than nine hours during construction,

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as reported in my earlier account, and three others that I watched briefly, only the female worked. Moreover, I have repeatedly seen a female pull material from an epiphyte-laden branch and carry it beyond view, followed by a male with empty bill. One female brought material and arranged it in her nest 33 times in six hours and ten minutes. On a cool, drizzly morning another female brought contributions to her nest 25 times in 1.5 hours. The most rapid building that I have seen was at this nest, to which the female came with material 11 times in a half-hour. Often the male follows his building partner to the nest, waits nearby while she carefully arranges what she has brought, then flies away with her. Both partners are usually silent while building proceeds. Rarely during nest construction the male seizes his mate's tail and holds tightly, while she tries hard to escape him. The struggle may continue until the two fall together to the ground. Each of two nests was built in four or five days of leisurely work.

The nest is a shallow, open cup, 6 to 8 cm in diameter by about 5 cm high. The concavity is 4.5 to 5.2 cm in diameter by about 2.5 cm deep. The slight structure is composed chiefly of whole dead dicotyledonous leaves, mostly between 2.5 and 8 cm long, exceptionally as much as 9 cm long by 4 cm broad. Mixed with the leaves, and helping to hold them together, are thin, curved, minutely spiny secondary rachises of the twice-compound leaves of *Mimosa myriadena*, a vigorous liana of the rain forest, and also fine, tough fungal hyphae, dry inflorescence stalks, and tendrils. The lining is composed of the same black and brown fungal filaments, carefully coiled down, and leaves reduced by decay almost to lacy skeletons. Cobweb binds the nest together and fastens it to the supporting twigs.

In three nests the first egg was laid no more than two or three days after building ceased. The earliest date for laying is 28 April 1969. In three completed sets the number of eggs was two, which in two of these sets were laid on consecutive days. At one nest the female passed the night on her first egg and laid the second between 5:35 and 6:40 next morning. The eggs in one set were long-ovate, dull white, finely speckled with reddish brown. On one of these eggs the speckles were densely crowded over all the thicker end, more thinly scattered over the thinner end. On the other egg the speckles were concentrated in a wreath around the thicker end and thinly scattered over all the remaining surface. An egg in another set (in which I found only the remains of the second egg) was pinkish white, faintly but densely flecked or mottled over most of the surface with a slightly darker, more brownish shade. Two eggs measured 21.8 by 14.7 and 21.4 by 14.3 mm.

In eight nests in the Valley of El General eggs were laid as follows: April, 1; May, 6; July, 1. In three of these nests the eggs were not seen, but the date of laying was calculated from the presence of nestlings. Apparently eggs are occasionally laid in August and even September, for one female fed fledglings at our feeder from 25 September to 5 October 1959; and two full-grown young, already able to feed themselves, received bits of plantain from both parents as late as 2 November 1951. In Trinidad

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four nests were found from May to July (French, 1973).

Only the female incubates. I watched one from 11:50 to 17:05 on 19 May 1954 and from 5:23 to 11:12 on the following day. Counting the two days as one, her active period lasted only about 10 hours, during which eight completed sessions ranged from 32 to 149 minutes and averaged 54.9 minutes. Nine recesses ranged from 6 to 20 minutes and averaged 12.2 minutes. This female incubated with a constancy of 81.8 per cent. At this nest, poorly situated for observation, I saw the male at the nest tree only once in the course of the day. On this occasion he did not feed his mate.

In 1977 I found a nest more favorably situated, 2.5 m up on a fork of a fairly thick, ascending branch of a calabash tree in the garden. It was set amid clustered sessile leaves that supported it laterally and concealed it well, but around this branch was a wide clear space that made it easy to follow the honeycreepers' movements. On the clear morning of 19 May the female, which had incubated through the night, first left the nest at 5:56, as the sun rose. From then until 12:04 she took seven sessions on the eggs, ranging from 19 to 69 minutes and averaging 41.6 minutes. Her seven absences ranged from 5 to 24 minutes and averaged 11 minutes. She incubated through the sunny morning with a constancy of 79 per cent—only slightly less than that of the Green Honeycreeper which I had watched 23 years earlier. She sat rather restlessly, often rising up, changing her position, and preening. Her mate came near the nest only three times and on at least two of these visits he fed her while she sat.

At one nest the incubation period was between 12.5 and 13 days.

The interior of the nestlings' mouths is red, as in tanagers and finches, and the flanges at the corners are white. Young birds bear sparse natal down.

On the morning of 26 May I watched the nest in the calabash tree from 4:55 to 11:00. The female brooded the two four-day-old nestlings 17 times, for intervals ranging from less than 1 minute to 16 minutes and totaling 81 minutes. Her intervals of brooding became shorter as the sunny morning advanced, and after 9:00 she sat in the nest for only a minute or less at a time. She started her day's activities while the light of dawn was still so dim that I could hardly see her, and at 5:05 brought the nestlings' first meal and removed a dropping. By 11:00 she had fed them 26 times. The male did not start to feed until 6:19, and did so only seven times in the first six hours of the day. Often I distinguished bright red objects, most probably arillate seeds of *Clusia*, in the bill of the approaching parent. At other times they brought insects, and often they came and fed so rapidly that I could not distinguish the food. Early in the morning the female carried away a white fecal sac in her bill. All other droppings were apparently swallowed. As usual, the parents were quite silent.

Five days later, on 31 May, I again watched this nest from 5:00 to 11:00. The female began to feed in the dim light of dawn and when the male first came with food, at 5:43, she had already delivered eight meals. During

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the first six hours of the day the two nine-day-old nestlings were fed 36 times by their mother and 14 times by their father, a total of 50 times, or at the rate of 4.2 times per nestling per hour. The most rapid feeding was in the first hour of the morning, when the female brought 10 meals and the male one. On 16 parental visits I distinguished red *Clusia* seeds in their bills, and probably they brought this food even more frequently. Some meals consisted of insects or dark objects that may have been berries. Both parents removed droppings, either swallowing them or carrying them off in their bills. In other honeycreepers, as in the Green, females feed nestlings more often than males do, often much more often (Skutch, 1954, 1972).

Although the nestlings still showed much bare skin they were not brooded the morning of 31 May, which was mostly sunny. They preened their sprouting plumage and briefly exercised their wings. A day later they were nearly feathered. Their mother brooded them on their last night in the nest, which they left on 3 June when 12 days old. After their plumage is fully expanded juveniles resemble the adult female but are duller.

SUMMARY

Green Honeycreepers frequent the upper levels of humid forests and neighboring clearings with scattered trees. Their diet includes insects, fruits, oil-rich arillate seeds, and nectar. Many of their food plants are listed.

They bathe in rain water that collects in tank bromeliads and cavities in trees. They "ant" in trees.

They utter a warblerlike *chip* and, when perturbed, a low, dry rattle. They have not been heard to sing.

They mob hawks and snakes, in company with other birds or alone. One male apparently mistook a curled, shiny green leaf for a green tree snake.

Not infrequently a male seizes a female by the tail, perhaps in an effort to obtain a mate. Occasionally a male takes firm hold of the leg or wing of a small bird of another species.

Males feed their mates before nesting begins and while the latter incubate.

The female builds the nest, a slight, shallow cup, composed largely of small dead leaves, and situated from 1.5 to 12 m up in a shrub or tree in a pasture or garden near woodland. Males accompany their building mates but do not help to build.

The set consists of two eggs, laid from April to July, but chiefly in May and, apparently, occasionally as late as September.

Only the female incubates, taking sessions that sometimes continue for two hours or more, and covering the eggs with a constancy of about 80 per cent. At one nest the incubation period was between 12.5 and 13 days.

The nestlings are brooded by the female and fed by both parents, with insects, berries, and large quantities of the arillate seeds of *Clusia* spp. As in other honeycreepers, the female brings food more often than the male. The nestling period is 12 days.



FIG. 11. Silver-throated Tanager, *Tangara icterocephala*.

Family THRAUPIDAE
SILVER-THROATED TANAGER

Tangara icterocephala

Since I wrote my earlier account (1954) of the Silver-throated Tanagers, these elegant yellow-and-black birds have continued to nest almost every year in the shrubbery around our house, enabling me to fill gaps in their life history. Like many other species of *Tangara*, this is a bird of treetops in rain forest, where it wanders widely with other small birds in search of fruits, but it takes kindly to neighboring clearings with scattered trees and shrubbery. Although I have seen it, in November and December, at sea level in the forests near Golfo Dulce in southern Costa Rica, it becomes more abundant as one ascends wooded foothills on the Pacific slope. Here, between 1,050 and 1,500 m, it is one of the most abundant tanagers in the fast-disappearing forests. Across the international boundary in the Panamanian Province of Chiriquí, it occasionally ascends to 2,300 m, according to Ridgely (1976) who cites a record of its presence, in November, at Almirante on the Caribbean coast of Panama. Probably the Silver-throat descends to the coasts after the breeding season, to escape the cold rains that deluge the mountains toward the year's end. I have no record of its nesting below 750 m. The species ranges from Costa Rica to northwestern Ecuador.

In my experience, Silver-throated Tanagers are less sociable than some related species, including the Golden-masked (*Tangara larvata*) and Speckled (*Tangara guttata*) Tanagers. Although I have seen pairs at all seasons, I have often watched solitary individuals, especially toward the year's end. Perhaps the pair bond, if not wholly dissolved, becomes looser after the breeding season. Although the sexes are often difficult to distinguish in species of *Tangara* that remain in close contact with their mates throughout the year, female Silver-throats, similar to males in coloration, are frequently decidedly paler. Never having seen Silver-throated Tanagers in flocks larger than a pair with dependent young, I read with surprise Ridgely's statement that on Cerro Campana, in central Panama, they are sometimes found in "large flocks of several dozen or more individuals." Perhaps a generously fruiting tree drew all these Silver-throats together. I have seen no indication of territorial defense in these birds which appear to be quite songless. I have never heard from them notes more melodious than a dry, nasal buzz and other weak, insectlike sounds.

FOOD

Like other species of *Tangara*, Silver-throats hunt for insects and other small invertebrates amid the foliage of trees or, more characteristically, amid the mosses, liverworts, and lichens that grow profusely over the limbs of trees in humid foothill forests. They cling, often head-downward, to upright

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branches and thin dangling twigs, or they work along a horizontal bough, bending down now on one side, now on the other, to see what they can find hiding on the lower surface. Sometimes they pull off moss or lichens to expose whatever lurks beneath.

Among fruits that I have seen Silver-throats eat are small wild figs, juicy purple berries of pokeweed (*Phytolacca rivinoides*), orange berries of *Citharexylum* trees, yellow berries of the epiphytic shrub *Lycianthes synanthera*, and, above all, little, deep purple, blue, or black berries of many shrubs and small trees of the melastome family, especially species of the huge genus *Miconia*. In the forest they peck into the large, bright red, juicy fruits of the arenilla, a tree of the myrtle family abundant at Los Cusingos. They join birds of many other kinds in stripping the tiny green fruits from the dangling spikes of the *Cecropia* tree. They peck pieces from the white arils that surround the large seeds of *Protium* trees; and they eat the small, massed, red or orange, arillate seeds of epiphytic small trees and shrubs of the genus *Clusia* and the epiphytic vine *Souroubea guianensis*. At the feeder they are attracted by bananas, of which the male sometimes offers morsels to his mate, busily helping herself to the same fruit, and they sip the juice of oranges cut transversely in half and laid on the board. Silver-throats vary their diet with green flowers and tender young fruits of cucurbitaceous vines, including the tacaco (*Polakowskia Tacaco*).

ROOSTING AND BATHING

I have only thrice found a Silver-throat roosting. In late October one slept about 3 m above the ground on a branch of an introduced flame-of-the-forest tree (*Spathodea campanulata*), where it was well screened by foliage above but fully exposed below. In August, years later, a Silver-throat roosted for a number of nights on a caña de India shrub (*Taetsia fruticosa* var. *ferrea*) in front of the kitchen window. It rested on a petiole about 2 m above the ground, close beneath a broad, arching leaf that formed a roof above it on rainy nights. For several nights in February 1968 a Silver-throat slept 2.5 m up in a shrub of *Palicourea guianensis*, its yellow breast turned toward a nest, 30 cm away, in which a Rufous-tailed Hummingbird (*Amazilia tzacatl*) brooded two nestlings. Although mated individuals of some tanagers, including the Golden-masked (*Tangara larvata*) and the Blue (*Thraupis episcopus*), often roost close together but not in contact, I searched vainly for mates of these three sleeping Silver-throats.

To bathe the Silver-throat sometimes seeks a hollow in a high branch of a tree where rain water has collected.

NEST

The approach of the Silver-throat's nesting season is not heralded by song. Nesting rarely begins in February but more often in March or April. Possibly many nests of Silver-throats are situated high in the forest, where I have never found one. Others are built on riverside trees, especially on

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the sotacaballo (*Pithecolobium longifolium*), or in vines growing over them, where I have discovered three, at heights of 1.8, 2.1, and about 11 m above the rocky channel of a mountain torrent, well out from shore. These may have been the sites that Silver-throats most often chose for their substantial, moss-covered, open cups before man so drastically transformed this valley. Now they frequently build in trees and shrubbery growing in clearings. The majority of the nests that I have seen were situated around our house in fruit trees and ornamental shrubs, including the orange, mango, calabash, itabo (*Yucca elephantipes*), the variegated croton, and gardenia. The most favored sites were among the bases of the broad red-and-green leaves of the caña de India and amid the thin, densely crowded, upright stems of the shrubby *Thunbergia erecta*. Farther afield I have found a few nests in trees in bushy pastures. The extreme range in height of 52 nests built above land was 1 to about 8 m. Nearly half of these nests (24) were 1.2 to 2.5 m up. Only five were below 1.2 m. Nine were 2.5 to 3.7 m; five 3.7 to 5 m; seven 5 to 6 m; and two above 6 m.

At about 8:00 on the morning of 29 April 1954, I saw a pair of Silver-throats fly into an orange tree, both bearing moss in their bills. One laid its load in a bare fork 1.8 m up. Then the second tanager passed its moss to the first, which deposited it in the same spot. I had the good fortune to witness a pair laying the very first pieces of a nest.

Although the male Silver-throat may sometimes help to start a nest, he rarely continues to build. In 17 hours of watching at six nests the males brought contributions to two of them a total of six times. At five other nests watched more casually I saw the male give some help at three; but only the female worked at two. At an additional nest, where the sexes were too similar to be distinguished, they brought 61 billfuls of materials in four hours. On 20 occasions both birds arrived together with material, from which it was clear that the male was taking a substantial share in the work of construction, bringing at least one third of the contributions.

More often than he builds, the male Silver-throat faithfully follows his partner back and forth on her trips to gather material, and from time to time he feeds her, either while she sits shaping the structure or near it. In 17 hours of watching at the six nests where the males brought little or no material, they fed their mates a total of 13 times. The male that brought material five times in 5.5 hours (while his mate did so 115 times) was seen to feed her six times in this interval. Doubtless, he gave her more food while the two were beyond view, as males often passed billfuls to their partners at the feeder. One male tried to feed his mate as she approached the nest with a big piece of leaf in her bill. Finding that with so full a mouth she could not take the proffered gift, he followed her to the nest and passed it to her after she had deposited her burden. While another female was building in a gardenia, her partner flew into the shrub with a fragment of food in his bill. Soon the female arrived with a piece of fruit, apparently of a guava, too big to swallow. The male took it from her and, after working on it for a while, part of the time on the ground,

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reduced it to swallowable size, then returned it to his mate, which ate it. Then both flew off together. The male that built most actively was not seen to feed his mate.

The nest is built in two stages, in which the female follows different procedures. In the first stage she brings much green moss, liverworts, fibers, and cobweb for the nest's massive foundation and outer wall. In this first stage she comes from beyond view with a billful of material, arranges it in the growing nest, then quickly gathers more from the mossy limbs of the supporting tree, but always a meter or more from the nest, for to remove it from close beside the nest would diminish its concealment. On a single visit to the nest tree she may add material to the nest from two to five or rarely as much as 10 times. One female added 51 billfuls on 23 visits; another, 34 billfuls on 11 visits.

As she passes from the first stage to the second, the building female mixes dry leaves with her green material. Soon she has enough of the latter and concentrates upon bringing dead leaves. Since few of these are available in the tree or shrub where she builds amid green foliage, she flies afar for them. Finally, she brings a few coarse fibers as inner lining.

Although, like most passerines, Silver-throats build most actively in the early morning, I have twice known one to work strenuously for an hour or so in late afternoon, after a shower that soaked her material and made it more pliable. At six nests where the females worked with little or no help from their mates, they brought 283 contributions to their nests, from nearby or afar, in 17 hours, or at the average rate of 16.6 per hour. In two hours of the early morning one female added 68 billfuls to her nest, or slightly more than one every two minutes. She interrupted her labor for intervals of only a minute or two, while she ate plantain at the neighboring feeder. For shorter periods she worked even faster, bringing 20 billfuls in 27 minutes then, after a two-minute meal, 15 billfuls in 18 minutes. In addition to flights to gather material, she spent much time sitting in the nest, arranging or shaping it. Few birds that I have watched have worked so hard.

At the nest where the male rather equally shared with his mate the task of building, both helped to shape the structure. Sometimes one of the partners passed its load to the other which sat in the nest, and at other times it carelessly dropped the moss on the growing accumulation. Both birds gave much attention to retrieving pieces that fell from the inadequate site, and to pulling loosely attached pieces back into place, at times continuing this occupation for three or four minutes. But, finally, the accumulation fell to the ground and the site was abandoned.

When a male gives little or no help he perches in silence near the nest, idly, or preening his handsome yellow plumage, while the female gathers moss from neighboring branches. Or he may search over nearby boughs for insects, which sometimes he presents to his toiling partner. When the female makes longer excursions to gather materials, the male follows her. Rarely he returns with a small contribution of material, which he passes

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to his mate as though he were feeding her. If she delays to take it from him, or if she remains long shaping the nest so that he cannot enter to deposit what he has brought, he may drop the piece. Occasionally a loitering male retrieves a leaf or bit of moss that falls from the nest, but as often as he replaces it he toys with it, and eventually drops it to the ground.

One nest was built in 3 days; two took 4 days to complete; four took 5 days; and one took 6 days. The structure is bulky for so small a bird. The foundation is composed of a great mass of green mosses and liverworts, with a few pieces of small-leaved ferns with thin, creeping rhizomes, such as diminutive polypodies and *Rhipidopteris peltata*. Mixed with the green material of one nest were many dry, branched inflorescences of *Cordia* sp. In this massive green cup is a shallow or deep hollow, lined with dry leaves, including nearly whole small leaves of dicotyledonous trees, grass blades, or strips torn from great monocotyledonous leaves such as those of *Heliconia* and *Calathea*. A thin mat of wiry fungal filaments or coarse fibers covers the bottom of the open cup. A nest now before me measures 10 cm in diameter by 6 cm high. The interior dimensions are 6 cm in diameter by 4.5 cm deep. This is a beautiful structure with a wreath of living polypody fern encircling the rim. Situated amid clustering foliage or mossy branches, these green nests are not easy to detect.

EGGS

In five nests the first egg was laid on the morning following the day on which the structure was finished. At two nests 2 nights and 1 day intervened between the cessation of building and the start of laying. At one nest the interval was 3 nights and 2 days; and at one nest it was 4 nights and 3 days. From the start of building, and assuming that it always began early in the morning, the number of days elapsed before the first egg appeared was 3 at one nest, 4 at two nests, 5 at four nests, and 8 at two nests. With a single exception, I have always found the eggs to be laid on consecutive days, the second about 24 hours after the first. They are laid in the early morning, from before sunrise to soon after sunrise. Twelve first eggs and 14 second eggs were laid before 7:00. At least 16 of these eggs were laid before 6:30, and at least 8 before 6:00. One first egg was laid between 5:15 and 5:35; another before 5:35. One second egg was laid between 5:25 and 6:10. Only one egg is definitely known to have been laid after 6:10, on a dark, drizzly morning. None of the 26 eggs of which I timed the laying was deposited after 7:00. Although bracketing the time of laying between two visits of inspection fails to reveal the precise minute at which eggs appeared, my records suggest that most eggs were laid between 5:30 and 6:15.

One female, whose first egg was lost during the day on which it was laid, deposited the second in the empty nest on the following morning, as Scarlet-rumped Tanagers (*Ramphocelus passerinii*) sometimes do. This second egg was destroyed on the day after it was laid. Each of 42 nests

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contained two eggs or nestlings. In one late nest the female apparently laid only one egg. I found her in the nest on the evening before she laid this egg, although I have not known a Silver-throat with the usual set of two eggs to occupy the nest in the night before she laid the second.

The eggs are dull white or grayish, mottled all over with brown, most heavily on the thicker end, where on some eggs the brown blotches conceal the ground color. The measurements of 12 eggs average 21.5 by 15.6 mm. Those showing the four extremes measured 23.4 by 15.9, 22.2 by 16.7, 20.5 by 15.5, and 21.8 by 14.3 mm. The newly laid eggs of one set weighed 2.9 and 2.7 gr. Both eggs of another set weighed 2.6 gr.

In 51 nests in the Valley of El General, from 1936 to 1979, eggs were laid as follows: February, 2; March, 6; April, 11; May, 10; June, 6; July, 5; August, 10; September, 1. The earliest of these eggs was laid before 25 February 1964; the latest on 8 September 1957.

INCUBATION

At nine nests that I visited at night between the laying of the first and second eggs, the single egg was not covered; the female slept elsewhere. Incubation hardly begins before the set of eggs is complete. It is performed by the female alone. In early May 1937 I watched for seven hours a nest situated near the end of a long, drooping branch of a sotacaballo tree, which held it far out over the rocky channel of the Río Buena Vista, only 2 m above the noisily rushing torrent. Omitting an hour when the Silver-throat was disturbed by a Bare-throated Tiger-Heron (*Tigrisoma mexicanum*) that rested on a rock near her nest, which under the weight of rain drops had sunk dangerously close to the swollen current, I timed 12 completed sessions on the eggs and an equal number of absences. The sessions ranged from 8 to 48 minutes and averaged 21.1 minutes; the recesses from 5 to 12 minutes and averaged 8.3 minutes. The tanager covered her eggs for 71.8 per cent of the six hours. On nearly half of her returns her mate escorted her to near the nest, and twice he fed her while she sat. After she was well settled on the eggs he flew beyond view.

On 29 May 1943 I watched another nest, situated in a calabash tree in front of my house, where the eggs had already been incubated for 10 days. In slightly more than five hours of the dark, threatening morning, the female took 10 sessions that ranged from 17 to 33 minutes and averaged 24.1 minutes. Her nine recesses varied from 4 to 14 minutes and averaged 7.2 minutes. She covered her eggs for 77.0 per cent of the observation period. On a rainy afternoon this tanager incubated continuously for 43 minutes. In seven hours of watching at this nest I often heard the male tanager, but saw him only once when he accompanied his mate as she returned and fed her as she was about to enter the nest. Probably he gave her more food while they foraged together; sometimes he passed banana to her at the neighboring feeder.

At 12 nests where I timed, within limits of a few hours, both the laying

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and hatching of the second eggs, none hatched in less than 13 full days. One hatched between 13 days 1.5 hours and 13 days 3.5 hours; another, between 13 days 0 hours and 13 days 7-1/4 hours. Most eggs took about 13-1/4 days to hatch. The few nests in which the incubation period was prolonged to the fourteenth day were so near the house that the female was frequently disturbed by human activities. It is of interest that Silver-throated Tanagers' eggs take a full day longer to hatch than do the larger eggs of the Scarlet-rumped Tanager (*Ramphocelus passerinii*). This may be because, being smaller, they cool more rapidly during the female's frequent absences from incubation. Possibly, also, the reason for this difference is that the eggs in the Silver-throat's smaller, less conspicuous nests are subject to less intense predation pressure, which appears to be the most powerful agent for abbreviating the incubation period.

Of 10 first nestlings, three hatched in the night, six in the forenoon, and one in the afternoon. Of 12 second nestlings, three hatched in the night, four in the forenoon, and five in the afternoon. Likewise in the Scarlet-rumped Tanager a larger proportion of second nestlings than of first nestlings hatched in the afternoon, and evidently for the same reason—because the eggs are laid early in the morning and the incubation period is often about six or seven hours more than a whole number of full days.

NESTLINGS

First morning.—At dawn on 2 June 1943 I entered a blind to watch a Silver-throat's nest in which both eggs had been pipped early on the preceding day. While the light was still so dim that I could barely follow the female's movements, she carried away, one at a time, four pieces of shells, thereby plainly indicating that the two eggs had already hatched. She appeared to feed the hatchlings, at first with very small items that she took from half a minute to a minute to deliver. Usually she brooded after each feeding. Although I heard her mate's voice, for a while he did not approach the nest. The female did not answer his calls, but once she flew from the nest when she heard him. Finally, at 6:33, an hour and a half after she became active at dawn, she repeated a slight, sharp, wiry note as he flew by the nest where she brooded. Possibly she tried to call his attention to the nestlings, with notes that to me sounded no different from those that I had repeatedly heard from her during the preceding days. Again at 7:23, when her mate entered a neighboring tree, she called to him, was answered, and the two flew away together.

When they returned 10 minutes later both carried food in their bills. The male went first to the nest, clung head downward to the thick, mossy branch that rose beside it, as I never saw the female do, and stretched far down to place food into the nestlings' gaping, red-lined mouths. After delivering this he departed. Thus, he first fed the nestlings about two and a half hours after their mother did in the dawn. Since he had long been in the habit of feeding his mate on the nest, his arrival with food at this

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time is not proof that he brought it for nestlings that he had not yet seen. Nevertheless, the fact that he preceded the female to the nest (as males regularly do while feeding young) suggests that he already knew that he had nestlings to feed, probably having learned by seeing the female carry food in her bill, rather than by vocal communication. This second possibility is difficult to reconcile with his long delay in feeding the nestlings, for he had been in vocal contact with her for at least two hours before he arrived with food.

In any case, the male was ready to feed his nestlings as soon as he saw them, with no delay between his first sight of them and his first delivery of food, as often occurs with avian fathers. Four minutes after the male Silver-throat first fed the nestlings he returned with another billful and gave it to his brooding mate, who rose up to pass it to one of the nestlings beneath her. After another seven minutes he came again with an overflowing bill, found his mate absent, and spent two minutes delivering the food directly to the nestlings which, after this generous meal, were too full to take more. Whether the male fed the nestlings directly or passed the food to his brooding mate, he always clung inverted well above the nest and stretched far downward. He persisted in a habit that he had formed earlier when he fed his building partner before her nest had a substantial rim on which he could stand. However, if the nestlings were slow to take what he offered, he might grow tired of his inverted posture and drop down to stand on the rim, as the female did when she arrived with food. When I ended my watch at 10:18 he had brought food to the nest nine times. Since daybreak the female had brought food about 16 times, twice as often in the two and a half hours before the male started to feed as in the subsequent two and a half hours, when he helped her.

In the five hours immediately following the removal of the eggshells the female Silver-throat brooded the nestlings for 19 periods, ranging from less than 1 to 21 minutes and averaging 10.1 minutes. Her 18 absences from brooding, on some of which she visited the nest to feed, ranged from less than 1 to 17 minutes, with an average of 6.6 minutes. In the first five hours of the morning she was on the nest 60.5 per cent of the time, as compared to 77.0 per cent of the time while she incubated four days earlier. After her mate helped to feed the nestlings her sessions of brooding lengthened substantially, from an average of 7.5 minutes during the first half of my watch to an average of 13.8 minutes during the second half.

Toward the end of the morning the female Silver-throat behaved surprisingly. Four times she picked up pieces of dry, papery leaf from the nest's lining and carried them away. Once she ate a piece of leaf; at other times she billed pieces, or tried to eat them, before dropping them back into the nest or flying away with them. Later I saw that some of the leaves stood up loosely around the nestlings and evidently interfered with her attendance on them, which was probably the reason why she removed some of them. I cannot recall having seen any other bird eat part of its nest, but Armstrong (1942) watched a Gannet (*Sula bassana*) which "picked up

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bits of weed stem and dirt from the nest, and, holding its beak on high, swallowed them with violent and vividly perceptible movements of the gullet. Not once or twice, but again and again, many times in succession, did she do this." He suggested that the Gannet was nervous in the presence of the observer. But, my Silver-throat was not as I was hidden in a blind that she accepted as part of her inanimate surroundings.

Care of older nestlings.—On 11 September 1978 I watched parents attend two four-day-old nestlings on a morning that began dark and foggy but became sunny after 7:00. The female brooded 11 times, for intervals that ranged from 3 to 17 minutes and averaged 10.5 minutes. She covered the nestlings for a total of 115 minutes, or 31.9 per cent of the first six hours of the day. When I again watched this nest through the cloudy morning of 18 September, the 11-day-old nestlings were not brooded.

I have no observations on nocturnal brooding at this nest. Another set of nestlings was brooded through the night only until they were 10 days old, when they were not quite covered dorsally with plumage. Possibly this early exposure was caused by some disturbance. However, at four other nests nocturnal brooding continued only one night longer, or until dawn of the eleventh day after the nestlings hatched, when they were well feathered. During the last four nights in the nest, these four broods slept without their parent. Even when rain fell as the day ended, nestlings were left exposed through their last night in the nest.

Possibly the female ceases to brood at night because the two nestlings so fill the little cup that there is no room for her. One Silver-throat slept on the nest's rim, beside rather than over her nestlings, when they were between 10 and 11 days old. She resembled a ball of yellow down lightly poised above the nest. Another Silver-throat, which continued to brood longer, perched on the nest's rim with her two nestlings half covered and half exposed, through their next-to-last night in the nest. During their final night she covered them completely, sleeping with her head forward instead of turned back and buried in her plumage. The mother of a single nestling also covered it during its last night in the nest. It is of interest that in both the Silver-throated and Scarlet-rumped tanagers nocturnal brooding is usually discontinued after the nestlings are 11 days old, although Silver-throats commonly stay in the nest three days longer than the larger tanagers.

The two four-day-old nestlings that I watched on 11 September were fed 25 times by the male parent and 32 times by the female, a total of 57 meals in six hours or at the rate of 4.8 times per hour for each of them. When these same nestlings were 11 days old their father brought them food 34 times and their mother 48 times, making a total of 82 meals in six hours. They were now fed at the rate of 6.8 times per nestling per hour. The least rapid feeding was in the first hour of the morning, 5:26 to 6:26, when only five meals were delivered; the most rapid in the following hour, when 20 meals were brought. In one feeding sequence the female delivered food, always white berries, six times in six minutes.

Unless the items were very small, food was carried visibly in the parents'

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bills, but often it was so mangled, or delivered so rapidly, that identification was difficult. The diet of the four-day-old nestlings consisted chiefly of adult or larval insects, with a small admixture of berries and arillate seeds. A week later these nestlings received about as much vegetable as animal food, including berries from a nearby shrub of *Palicourea guianensis* and bright red objects that were apparently arillate seeds of *Clusia*. One berry was so large that a nestling could not swallow it until its father had mashed it well.

The method of delivering the food is interesting. Each parent always gave directly to the nestlings everything it brought. If the female happened to be brooding when her mate arrived, she promptly left the nest so that he could feed the young. Taking the two mornings together, the two parents arrived with food simultaneously, or in rapid succession, 33 times, and on 30 of these occasions the male fed the nestlings before the female. Once the female, about to deliver food, stood aside when her mate alighted near her, and did not feed a nestling until after he had done so. On the three occasions when the female fed first she probably did not see the male approaching from the other side of the croton shrub that supported the nest. The precedence of the male in feeding saved motion when the female would brood immediately after delivering food; and this habit, once formed, persisted long after diurnal brooding ceased.

Both parents removed droppings. When the nestlings were four days old the female swallowed 13 of them and carried away one in her bill. The male swallowed four. When the young were 11 days old each parent carried six fecal sacs away in its bill; the male ate one that broke and fell into the nest as he was removing it.

Development and departure.—Silver-throats hatch with sparse gray down and tightly closed eyes. The inside of the mouth is red and the flanges at the corners are white. On the culmen, just inward from the tip of the bill, is an egg tooth so minute that it easily escapes detection. Instead of falling all at once, like the egg teeth of certain nonpasserines, this tiny protuberance gradually disappears. When one nestling was nine days old its egg tooth had vanished, while that of its sibling of the same age had been reduced to a minute whitish spot which persisted at least until the young tanager was 12 days old. When two other nestlings were 10 days old their egg teeth had nearly disappeared; a slight irregularity on the smooth culmen, visible with a pocket lens, revealed where they had been.

Like other passerine nestlings, Silver-throats stretch up their gaping mouths, not only when their parents arrive with food but also when a hand or some other object moves above them, when the nest is slightly shaken, or when they hear a weak sound. They react to stimuli which they seem to associate with the arrival of a food-bearing parent. As they grow older they become more discriminating, gaping vigorously to their parents but crouching down, as though in fear, when some strange object approaches them. I was interested to learn at what age the Silver-throats' reactions to me would undergo this change.

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Two seven-day-old nestlings, already open-eyed, stretched up widely open, red-lined mouths when I held a hand above them, and likewise when I made a clucking sound with my tongue. At eight days of age their behavior was the same. Early on the following day both gaped vigorously to my hand after being aroused by clucking, but later on that day one gaped persistently, while its sibling crouched down. At 10 days of age both of these nestlings gaped repeatedly to my hand. I then removed one from the nest for examination, and immediately afterward the other cringed when I held my hand above it. Nevertheless, after I had removed and replaced this second nestling, it again gaped to my hand.

Another pair of 10-day-old nestlings gaped vigorously and persistently, even when I opened and closed my hand above them. Their nest was at eye level, and they probably did not see my face. When I held over the nest a mirror, in which I could see them and they in turn could see my eyes or face, they immediately crouched down and clung to the bottom of the nest. Even an hour later, I could not induce them to lift up their heads. On a number of visits next morning these nestlings, now 11 days old, crouched instead of gaping when they saw my hand, but that same afternoon they gaped hesitatingly. Their reaction evidently depended, in part, on how hungry they happened to be. The other pair of 11-day-old nestlings gaped for me in the morning but not in the afternoon. The transition from consistent gaping to consistent crouching takes several days, during which the nestlings' reaction to human disturbance is unpredictable. When they are 12 days old, well feathered, at least dorsally, and with good vision, the transition is completed, and nestlings consistently press themselves down as low as they can in the nest when their visitor is not a parent. At this stage disturbance may make them jump prematurely from their nest.

Of 17 nestlings whose age of departure I know, three, including one raised alone, left the nest on the fourteenth day after that on which they hatched. Thirteen left on the fifteenth day. One, that hatched in the afternoon, quit the nest early on the sixteenth day when it was between 15 days 14 hours and 15 days 19 hours of age. The usual nestling period is 15 days. All but one of the 17 nestlings left the nest, spontaneously, before the middle of the forenoon. One left between 12:00 and 15:00. Two 15-day-olds, that hopped from their nest in a *Thunbergia* before 8:00 in the morning, remained for a while amid the densely crowded stems of the shrub, then returned to their nest, to abandon it finally in the early afternoon.

LATER BROODS

In a long breeding season that extends from late February or March to September, Silver-throats have time to raise at least three broods, but I have definite evidence for only two. In four cases a pair started a new nest while at least one of the parents continued to feed a fledgling or two from an earlier nest. In two of these new nests eggs were laid 11 and 20 days after the young left the previous nests. Another female laid

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again only eight days after the departure of her first brood, but I do not know whether her fledglings survived. Another, whose nestlings flew on 1 June, built a new nest only 1.5 m from the first and laid again on 24 June. Still another, whose brood left on 14 June, laid in a new nest near the first on 29 July; and one whose nestlings left on 16 July laid again on 1 August. These few records suggest that the interval between broods is most variable. I have no data to show how soon after eggs or nestlings are lost a replacement set is laid. I have not known Silver-throats to use the same nest for two broods.

YOUNG AFTER FLEDGING

After quitting the nest the young Silver-throats disappear amid the foliage, while the parents carry food to them, often billfuls of banana from the feeder. Soon they follow their parents to the tree that holds the board. As big as the adults but dull greenish yellow instead of bright yellow, they rest with quivering wings and harsh buzzing and rasping notes on a branch above the table, while the parents bring them food. After a few more days they stand on the board while the parents feed them; and presently they help themselves to banana. In several years I have seen young Silver-throats still being fed in October, once in the last week of this month. Although at first both parents feed flying young, one, usually the female, often continues to do so longer than the other. After the young are well able to take care of themselves they leave their parents, which often go their separate ways toward the year's end.

The young pass their first breeding season in a plumage similar to, but duller than, that of older birds. Yearlings acquire the bright yellow of the adult plumage by means of a complete postnuptial molt.

NESTING SUCCESS

In Table 4, I have analyzed separately the success of 35 nests of known outcome, at whatever stage they were found, and that of 24 of these nests found before incubation began. As expected, the sample that includes nests found with eggs already well along in incubation, or with nestlings, shows higher success, 54.3 per cent, than the sample that includes only nests found before incubation began, 50 per cent. The latter were exposed to predation and other losses for a longer interval while under observation. However, the difference is small, probably because most of the nests in the larger sample are also included in the smaller sample. As in other studies, loss of eggs, 40.4 percent, was very much greater than loss of nestlings, only 25 per cent, although both were in the nest for the same interval of 14 or 15 days (including, for the eggs, the day when the first was laid), and activity at the nest was very much greater in the nestling period than in the incubation period. Nests that escape destruction until the eggs hatch because they are well built, well concealed, or where no predators are active, are already a selected set, with a much better probability of success than nests with newly laid eggs.

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TABLE 4
Nesting Success of Silver-throated Tanagers

All nests of known outcome	35
Nests successful (at least 1 young fledged)	19
Nests failed completely	16
Per cent of nests successful	54.3
No. of above nests found before incubation	24
Nests successful (at least 1 young fledged)	12
Nests failed completely	12
Per cent of nests successful	50
Eggs laid in 24 nests	47
Eggs hatched	28
Per cent of 47 eggs hatched	59.6
Young fledged from 47 eggs	21
Per cent of 47 eggs producing fledglings	44.7
Per cent of 28 hatchlings fledged	75

It is instructive to compare the success of the Silver-throats' nests found early with that of the Scarlet-rumped Tanagers in the same category (Table 7, p. 257). Most of these nests of both species were in our garden or adjoining pastures, where they were exposed to the same perils. Their successes, 50 and 44.3 per cent, do not differ greatly. The slightly higher success of the Silver-throats' mossy nests may be attributed to their smaller size and better assimilation to their setting. None of the predators on these nests was surprised in the act, but they were most probably the same as those that destroyed the Song Tanagers' nests, chiefly snakes and squirrels. Losses other than by predation were small. One nest tilted under a heavy rain and spilled out the eggs. Only one of 43 eggs that escaped destruction failed to hatch.

SUMMARY

Silver-throated Tanagers wander widely through treetops of foothill rain forests. They often enter neighboring clearings with scattered trees and shrubbery to forage and to nest. Although at least some pairs remain together at all seasons, the pair bond appears to be looser than in other species of *Tangara*.

These tanagers eat many fruits and arillate seeds, and they search over mossy boughs and twigs for small invertebrates.

They roost singly amid foliage, and bathe in rain water that collects in hollows in high branches.

The nest, a substantial mossy cup, is built in a shrub or tree, sometimes above a mountain torrent, at heights ranging from about 1 to 11 m. Nearly half of 52 nests were 1.2 to 2.5 m up. The female does most or all of the building. Males accompany and sometimes feed the building female, but they only rarely give more than token assistance. Nests are finished in four or five days, rarely longer.

GOLDEN-MASKED TANAGER

In the Valley of El General, laying begins in late February, peaks in April and May, and continues until September. The first egg is often laid on the day after the nest is finished, but sometimes two or three days intervene. The set regularly consists of two eggs, laid early in the morning of consecutive days.

Only the female incubates, with a constancy of about 72 to 77 per cent. Her mate escorts her to the nest and occasionally feeds her. The incubation period is about 13-1/4 days.

Only the female broods the nestlings, but the parents take nearly equal shares feeding them. One male started to feed about 2.5 hours after his mate removed two empty shells at dawn. When the two parents arrive together at the nest the male almost invariably feeds first, whether or not the female will stay to brood. At first the nestlings receive chiefly insects, but fruit becomes prominent in their diet as they grow older. Young nestlings were fed at the rate of 4.8 times per hour for each of them; older ones at the rate of 6.8 times.

Young nestlings gape to a human hand; older ones crouch down in the nest. The transition from a positive to a negative response takes several days, during which the nestlings' behavior is unpredictable. Not until they are 12 days old and well feathered do the nestlings consistently crouch when so tested.

Some nestlings are brooded nightly until they leave the nest, but many are alone on their last three or four nights.

Most nestlings leave spontaneously before mid-morning of the fifteenth day after they hatch. A few leave on the fourteenth or sixteenth day.

Two, and possibly three, broods are raised in the long breeding season. Observed intervals between the departure of a brood and the laying of the first egg of another brood ranged from eight to 45 days.

Of 35 nests found at all stages, 54.3 per cent were successful. In 50 per cent of 24 nests found before incubation began at least one young fledged.

GOLDEN-MASKED TANAGER

Tangara larvata

Clad in golden buff, blue, turquoise, black, and white in an intricate pattern, the Golden-masked, or Golden-hooded, Tanager is one of the loveliest species in a lovely genus. The sexes of this 13 cm bird are often indistinguishable, but in some pairs the female is slightly paler than the male. From southeastern Mexico it extends along the whole rain-forested Caribbean side of Middle America to Darién. Absent from the drier Pacific slope of northern Central America, it first occurs on the western side of the continent about the Gulf of Nicoya in Costa Rica and was formerly abundant among the vanishing rain forests of the southern Pacific slope of that country, whence it extends through Panama to western Colombia and Ecuador. In Guatemala it appears to be confined to the northeastern and northern lowlands below 400 m

GOLDEN-MASKED TANAGER

(Land, 1970), and in Honduras it has not been recorded above 750 m (Monroe, 1968). In Costa Rica I have met it from sea level up to about 1,500 m, and it ranges as high in western Panama (Ridgely, 1976). From the rain forests, where Golden-masked Tanagers wander through the upper levels with other small frugivorous birds, they enter second-growth woodlands, shady plantations, and gardens with fruit or shade trees and abundant shrubbery. To nest they appear to prefer shady clearings and forest edges to the interior of closed woodland.

Since I wrote my earlier account of this tanager (1954), I have seen certain aspects of its behavior that had escaped my attention during many years of familiarity with the bird, and I have learned more about its food, but I have little new information on its reproduction.

FOOD

Among the fruits that I have seen Golden-masked Tanagers eat are small figs, and berries of *Sabicea costaricensis* (Rubiaceae), *Lycianthes synanthera* (Solanaceae), mistletoes (Loranthaceae), and of the abundant trees, shrubs, and undershrubs of the melastome family, including *Miconia trinervia*, *M. hyperprasina*, and *Clidemia sericea*. Like other tanagers and honey-creepers, they are eager for arillate seeds, rich in oil. Among those that I have seen them take are seeds of *Zanthoxylum* sp., *Alchornea lotifolia*, *A. costaricensis*, *Souroubea guianensis*, *Clusia* spp., and *Casearia sylvestris*. On cecropia trees, Golden-masked Tanagers find two kinds of food, the dangling, green fruiting spikes and the tiny white protein bodies that dot the furry brown bases of the petioles of trees not heavily infested by *Azteca* ants, which depend upon these corpuscles for nourishment. Bananas on the feeder, or a ripening bunch in a plantation, vary the Golden-masks' diet; and they sip the juice of oranges made available to them by cutting the fruit open. They search for insects and spiders on mossy branches and catch flying insects, especially slowly fluttering sexual termites, on short aerial sallies.

VOICE

Like all the other species of *Tangara* that I know well, the Golden-masked Tanager is poorly endowed vocally. Its most frequent note is a sharp, dry *tick*, which is rapidly repeated by both sexes and appears to serve chiefly to maintain contact between a male and female, which at all seasons are almost constantly together, whether they fly, eat, build a nest, or feed young. They repeat this tuneless ticking both in flight and at rest.

Until 1960 I had heard no sustained performance and hesitated to call this utterance a song. But in mid-February of that year a Golden-masked Tanager repeated it so persistently in the trees in front of our house that I could no longer doubt that the bird was singing, to the best of his ability, yet failing to achieve the least melody. Beginning in the dim light at about 5:30, he (I assume the sex) often sang intermittently until sunrise, about half an hour later. The very rapid series of low, dry *tick*'s lasted three

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or four seconds and was repeated at irregular, rather long intervals. Between songs the tanager moved around much and sometimes flew back and forth between neighboring trees. Until mid-August he continued to perform every day at dawn, although for shorter intervals as the year advanced. On 24 February a pair of Golden-masked Tanagers started to build a nest in the calabash tree beneath the taller tree where the male chiefly sang; and in June a second brood was raised in an itabo (*Yucca elephantipes*) not far from the singing tree.

In the following year, 1961, the tanager again started in mid-February to sing at dawn in the same trees in front of the house. Now I could hear another Golden-masked Tanager singing in the distance. Later in the day I sometimes heard this same lustreless song near the house and farther afield. In more recent years these tanagers have become less abundant and I have not heard them sing at dawn. Like other birds with slight musical ability, especially the American flycatchers, the Golden-masked Tanager performs chiefly at daybreak. But, unlike many flycatchers and other dawn-singers, he has no special utterance for the twilight. His vocal ability is so slight that he employs similar dry *tick*'s as a song that evidently proclaims an at least loosely held territory, as contact notes, and, when nest or young appear to be threatened, as alarm or warning notes. In this last context the ticking becomes exceedingly rapid. Although, of the species of *Tangara* that I have heard, the Golden-masked Tanager sings most persistently, at least at dawn, the Bay-headed (*T. gyrola*) is the best songster, but by no means a brilliant one.

SOCIAL RELATIONS

The social relations of Golden-masked Tanagers are confusingly ambivalent. It is rare to see more than three or four flying together. Sometimes this number alight on the feeder and eat peaceably, but on other occasions, when more than two are present, one chases another. Most often I have found only a pair roosting in the same tree, a few centimeters to a meter apart, never in contact. On several occasions, however, I have watched a number enter a densely foliated tree at the day's end. Once, late in the year, at least 17 roosted in two neighboring trees, with 11 on one low branch (Skutch, 1954).

When I wrote this earlier account I could report no fighting, but I have since discovered that, like Scarlet-rumped Tanagers (*Ramphocelus passerinii*), Golden-masks do on occasion resort to violence. I had lived among them for 30 years before I noticed a serious conflict. As I passed near the feeder on the morning of 14 February 1962, a number of downy feathers drifted earthward. Beneath them were two Golden-masked Tanagers clutching each other on the lawn. They promptly arose and flew off with two others, four in all.

I have seen no more contact fighting between Golden-masked Tanagers, but on a number of evenings in July 1962 two pairs flew around among

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the trees beside our house, mildly chasing each other and incessantly repeating their ticking notes. These pursuits often continued for from a quarter to half an hour, or even more, before the tanagers flew off, two by two, in different directions. During the following months this evening performance was repeated many times; I last recorded it on 24 December. Apparently it is by means of such interactions, and by singing at dawn, that Golden-masked Tanagers space their nests widely—I have never found two close together. Yet Silver-throated Tanagers (*T. icterocephala*), which have even poorer voices than the Golden-masks, and which I have never heard singing nor seen quarreling, somehow also avoid clustering their nests.

Although Golden-masked Tanagers commonly live in monogamous pairs throughout the year, I have on three occasions (in 1937, 1940, and 1960) watched trios in fully adult plumage bringing food to young, coming and going together with no evident friction. On the first occasion they fed a single young that had apparently left the nest prematurely and could scarcely fly. On the second occasion the three attended a nest so high and well screened by foliage that I could not learn how many nestlings it contained. On the third occasion the low nest held one nestling and one unhatchable egg. I could learn neither the sex of the helper nor its relation to the parents. At four nests I have found a single Golden-masked Tanager in greenish juvenal plumage helping the parents, rather sporadically, to feed nestlings that were probably its younger siblings. Assuming that these young helpers belonged to the parents' preceding brood, one was one and a half months old and one three months old.

In addition to helpers of their own species, nesting Golden-masked Tanagers sometimes have an assistant of another kind. In May 1953 a female Tropical Gnatcatcher (*Polioptila plumbea*) fed and brooded nestling Golden-masked Tanagers, and also cleaned their nest, as told in detail in my life history of the gnatcatcher (1960). Although the parent tanagers appeared not to welcome this unsolicited cooperation, at first their opposition was mild. Only after the gnatcatcher tried to keep the parents away from their nest did they attempt to drive her away, but the spirited pursuits never resulted in contact. Taken all together, my observations show that Golden-masked Tanagers are mild, pacific birds, tolerant of other individuals of their own or different species, yet capable, on occasion, of being aroused to violent action.

NEST

On Barro Colorado Island in the Panama Canal Zone I found a pair of Golden-masked Tanagers starting a nest as early as 10 February, but in the Valley of El General building begins somewhat later, my earliest dates being 22 February in 1947 and 1973, and 25 February in 1943 and 1960. In most years I have noticed no building before March. The sites chosen for the nest vary greatly in character and height. The nest may be placed in a fairly thick, preferably mossy fork of a small tree or near

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the end of a slender branch, amid clustering foliage. Often an orange or lemon tree, with protecting thorns and dense foliage, is favored. Nests in our garden are set amid the bases of the crowded, slender, sharp-pointed leaves of the itabo, where they are difficult to see, and among the broad, green-and-red leaves of the caña de India (*Taetsia fruticosa* var. *ferrea*). An unusual late nest was built between an ear and the stalk of a dry maize plant, standing at the edge of a rice field. Brown leaf blades that draped the stem sheltered it above.

Sometimes these tanagers select a more enclosed situation. In El General three nests were excellently concealed in the midst of bunches of green bananas hanging where they grew in small plantations, and another was in a cluster of the small plantains known as "dominicas." Such a site is not unusual, for in Panama Eisenmann (1957) also found a pair nesting in a bunch of bananas. Two nests were in the hollow ends of high dead branches. One pair in Costa Rica placed its nest quite out of sight in a cavity, probably carved by woodpeckers, about 30 m up in a dead trunk. In Panama Eisenmann likewise found a pair nesting in an old woodpecker's hole. He watched a tanager enter a deserted, pendent pouch of a Chestnut-headed Oropendola (*Zarhynchus wagleri*), through an opening near the bottom rather than through the oropendola's entrance far above at the top of the nest. In this pouch woven by a much bigger bird, the tanager was incubating two eggs, as Eisenmann learned when a storm blew down the nest.

At Los Cusingos I watched a pair of Golden-masks build amid the curled dead leaves that draped the trunk of a slender young cecropia tree growing at the edge of a thicket. In contrast to these hidden nests, one was tucked between a twist of a thick liana and the dead trunk that the vine embraced. In this exposed, shadeless site at the forest's edge, a pair fed nestlings. With the exception of a nest in the end of a broken-off branch of a tree standing in an opening in a small patch of forest, all the nests that I have seen were in shady dooryards or pastures, plantations, streamside trees, rows of living fence posts, tall open thickets, or at the woodland's edge. Of the tanagers that I know well, only the Blue Tanager (*Thraupis episcopus*) selects a somewhat greater variety of sites, and only this species and the related Palm Tanager (*T. palmarum*) have the same tendency to conceal their nests in crannies.

Nests of which I have recorded the height were situated as follows:

Under 2 m	4 nests
2 to 3.5 m	32 nests
3.5 to 5.5 m	13 nests
5.5 to 7.2 m	10 nests
7.2 to 9 m	4 nests
9 to 15 m	5 nests
15 to 28 m	1 nests
Total	69 nests

Both sexes build, as I have seen at more than a dozen nests. They fly

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back and forth together, seeking and bringing material. Usually each places its own contribution and sits in the growing structure to arrange it, but sometimes one passes its billful to the other who is so engaged. If one arrives at the nest with empty bill, this is probably because its partner has found suitable material first and, rather than be left behind, the other has followed with nothing. Building is accompanied by much sharp ticking, and at times a tanager utters a rapid series of ticks while sitting in the nest. At intervals the male feeds his mate. Although visits to the nest tend to be rather widely spaced, they continue through much of the day. Two nests were completed in four days and three others in six days, but one pair took 12 days to finish their structure.

Juveniles in greenish plumage sometimes make gestures of building. On 8 June 1956 I watched an adult with two young in juvenal plumage, near the nest in which, apparently, they had been raised in April. The adult pulled a fiber from a nest that a Blue Honeycreeper (*Cyanerpes cyaneus*) had recently built but in which, as far as I could learn, she had never laid an egg. Then one of the young tanagers approached this nest and tugged at a long, strong fiber. When it resisted the tanager hung on it with closed wings, as passerines of various kinds not infrequently do to detach recalcitrant objects. The juvenile finally obtained a strand, only to drop it instead of carrying it away. The other young tanager sat briefly in the scant remnants of the honeycreeper's nest and made shaping movements. I failed to discover the new nest that these tanagers were evidently building. On another occasion a juvenile accompanying building adults plucked material but failed to take it to the nest.

The completed nest is a compact open cup. If built in a mossy crotch it is likely to be covered with much green moss, liverworts, and living pieces of delicate creeping ferns, all of which assimilate it to its setting. In other nests the outer layer consists of brown fibers and strips of dead leaves. Fine rootlets, thin curving rachises of small compound leaves, coiled tendrils, and pieces of herbaceous inflorescences are also found in the outer walls of nests. The middle layer is usually composed of flakes of papery bark or small dead leaves. The lining consists of fungal filaments that resemble horsehair, threadlike secondary rachises of mimosa, and similar fine materials. Most exceptional was the nest in the dry maize plant, which contained much brown corn silk in the foundation and outer wall, with a small admixture of delicate filmy ferns, polypody ferns, and liverworts. The inner wall consisted of many layers of dry, partly decayed fragments of maize leaves, interspersed with black fungal strands, which predominated in the lining. Much cobweb is used to bind the nests' materials together and fasten them to their supports.

EGGS

A day or two after the completion of the nest the female tanager lays her first egg. One pair continued to add to their nest on the day preceding

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the deposition of the first egg. Eggs are usually laid early in the morning. Three first eggs were laid before 6:10. Six second eggs were laid before 7:00; three of these eggs before 6:30. Somewhat exceptional was the female that deposited her first egg between 5:35 and 6:00 but did not lay her second egg until after 7:25, but before 11:25. Another female laid her second egg in the interval 7:20–8:55. In 42 nests the full set consisted of two eggs. In four nests I saw no more than one egg, but in each case another could have been lost. I cannot exclude this possibility even in the case of the one-egg nest that I kept under observation during the period of laying for, as I have seen in other tanagers, including the Silver-throated and Scarlet-rumped, the second egg is sometimes laid in a nest from which the first has already been lost. Without frequent checking the replacement of the first egg by the second is readily overlooked.

The eggs are dull white or pale gray, thickly sprinkled all over with fine or coarse flecks of brown or chocolate that are usually heaviest and most concentrated on the large end, where they may almost conceal the ground color. Some eggs have also a few black spots, others have the ground suffused with brown. The measurements of 25 eggs average 20.2 by 14.8 mm. Those showing the four extremes measured 21.4 by 15.5, 19.1 by 14.3, and 19.4 by 13.9 mm.

In 63 nests in the Valley of El General, eggs were laid as follows: February, 1; March, 13; April, 14; May, 20; June, 6; July, 5; August, 2; September, 2. A nest at about 1,200 m on the Pacific slope of extreme southern Costa Rica held nestlings on 13 May.

INCUBATION

Only the female incubates, starting after she lays her second egg. In 1935 I watched a nest on Barro Colorado Island for six hours, during which the female took six sessions ranging, in no regular order, from 10 to 64 minutes and averaging 29.3 minutes. Her six recesses varied from 6 to 29 minutes and averaged 16 minutes. At a Costa Rican nest watched for eight hours the female took 15 completed sessions that varied from 6 to 51 minutes and averaged 18.9 minutes. Her 17 recesses ranged from 2 to 17 minutes, with an average of 7.9 minutes. At another Costa Rican nest watched for 10 hours the female's 20 sessions ranged from 2 to 47 minutes and averaged 22.6 minutes. Her 20 recesses fluctuated from 2 to 11 minutes and averaged 7.3 minutes. These three females incubated with a constancy of 64.6, 70.5, and 75.6 per cent. It is of interest that for the female with the lowest constancy I recorded the longest session and the highest average length of sessions; but her recesses averaged slightly more than twice as long as those of the other two females. The 51-minute session of the second female, taken during a heavy shower, was almost twice as long as any that she took in clear weather.

Each male sometimes accompanied his mate as she returned to the nest, but often he stopped some distance away. Usually he remained beyond

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sight and hearing while she incubated. Rarely he returned to call her from her eggs. Perching in a neighboring tree, one male uttered a long, rapid series of *tick*'s, and was answered with similar notes by his sitting partner, which after two minutes joined him on a foraging expedition. Rarely the male comes to inspect the nest. One male fed his mate, at or near the nest, thrice in the course of eight hours. This and other males may have fed their mates while the two sought food together.

From 12 to 26 hours after the first minute fracture is detectable on or near the widest part of the egg, the hatchling pushes off the severed cap and escapes. At the nest on Barro Colorado the incubation period was only 13 days, but in the cooler Valley of El General it has been longer, slightly under 14 days at one nest, 14 days and 2 or 3 hours at another, and 15 days at one nest.

NESTLINGS

While her eggs hatch beneath her, the female sits restlessly, constantly rising up to look down into the nest. Before long she eats first one part, then the other, of an empty shell. As I saw at two nests, she may leave and return several times before she brings food. Although her mate is in vocal contact with her, and often flies with her, he apparently does not learn that his offspring have hatched, and he does not bring food for them until he has seen them. When, accompanying his mate on her returns to the nest, he happens to view the hatchlings, he promptly finds something for them. At one nest both parents first brought food 50 minutes after the female ate a shell in the dim light of dawn, telling me that the first young tanager had hatched. The male found and delivered a spider almost immediately after he first saw the hatchling. At another nest, where both eggs hatched very early, the female ate a shell, apparently of the second egg to hatch, at 5:31 and she first brought food at 6:25, on her fourth return to the nest. At 7:35 the male, resting 60 cm away, watched attentively while his mate delivered food. Then he promptly found an insect and brought it to the nest, two hours after his mate ate the last piece of shell.

Soon both parents bring food frequently. At the first of the above-mentioned nests, where the first egg hatched at daybreak, the second hatched at about 8:48. In the first five hours of the morning the male brought food 12 times and the female 4 times. When he found the young uncovered he fed them directly; but if the female was brooding he passed the food to her. Then she rose up to feed the nestlings or, if they were not hungry, she ate the morsel herself. In the five hours she brooded 10 times, for periods ranging from 2 to 36 minutes and averaging 17.3 minutes. Her 12 absences from the nest varied from 4 to 25 minutes and averaged 8.5 minutes. Thus, she brooded for 67.1 per cent of the time, which is about the same as a Golden-masked Tanager's constancy while incubating.

At the second nest, where both nestlings had hatched by daybreak, they were fed more often but brooded less than at the first nest. In the four

and a quarter hours between her first feeding at 6:25 and the end of my watch at 10:41, the female brought food 21 times. In the three hours between his first feeding at 7:38 and 10:41, the male delivered food 12 times. The female brooded 20 times, for intervals ranging from 1 to 11 minutes and averaging 5.8 minutes. Her 21 absences varied from 2 to 19 minutes and averaged 8.7 minutes. She brooded only 40 per cent of the five hours following her first departure from the nest before sunrise.

The tiny insects and spiders that the parents brought to newly hatched nestlings were carried invisibly, apparently inside their mouths or throats. They were not regurgitated from deeper in the alimentary tract, for I saw none of the muscular straining that accompanies this act. Often the insect had been well mashed in the parent's bill.

At the nest where the male brought food so promptly, I watched for five periods of one hour each, well distributed between the fourth and fourteenth days after the two nestlings hatched. In these five hours the slightly brighter male brought food 36 times and the female 29 times, a total of 65 times, or 6.5 times per nestling per hour. The number of feedings in single hours varied from 9 to 16. After brooding ceased the two parents nearly always came to the nest tree together, bringing food. Then the male invariably went first to the nest and fed the nestling, while his mate, holding her offering, flitted impatiently among neighboring boughs. As soon as he finished feeding she advanced to the nest to deliver what she had brought; then the two flew away together. I saw this sequence many times, not only during my hour-long watches, but likewise at odd intervals, as the nest was readily visible from my porch. Rarely, when the two came together, only one had food, doubtless because it had found nothing suitable when its partner, which had searched more successfully, started to fly toward the nest with a billful, and the other would not be left behind. So strong was the female's impulse to accompany her mate that occasionally, when he did not wait after he had fed the nestlings, she followed him carrying away what she had brought for them.

In several other tanagers that I have watched, including the Silver-throated Tanager, Speckled Tanager (*Tangara guttata*), Yellow-crowned Euphonia (*Euphonia luteicapilla*), White-vented Euphonia (*E. minuta*), and Golden-browed Chlorophonia (*Chlorophonia callophrys*), all of which commonly fly in pairs when attending their nests, the male consistently precedes the female in feeding the nestlings. When the female will remain to brood, this arrangement avoids lost motion; if she fed first she might have to withdraw from the nest to permit her mate to feed, then return to it. After daytime brooding ceases, the utility of this order of precedence is lost. In contrast to the aforementioned small tanagers, male and female of the larger Scarlet-rumped Tanager come independently to feed their nestlings.

In June 1946 a pair of Golden-masked Tanagers feeding nestlings in a calabash tree were assisted by a juvenile in transitional plumage, that had evidently been reared in a neighboring nest in May and was now about six weeks old. When I first noticed this greenish youngster helping at its

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parents' nest, it was most diligent, bringing food 17 times in two hours, during which the parents fed the nestlings 33 times. In the hour from 6:20 to 7:20 on 22 June the two nestlings were fed by their three attendants a total of 28 times, an unusually high rate, and in the following hour, 22 times. Often all three attendants arrived together, then flew away together after delivering what they had brought. At other times the young helper came alone. It did not bring such large billfuls as the adults usually brought. Often I could distinguish nothing in its bill when it went through the motions of feeding the nestlings, but at other times I detected a small morsel. All three attendants often carried billfuls of banana from the feeder to the nest.

A few days later, perhaps because engaging in an adult occupation had lost its novelty, the young helper brought food much less often than at first. In three and a half hours on 26 and 27 June it visited the nest only six times, while the parents together brought food 51 times. The helper often followed the parents to the nest without bringing anything.

In late June 1948, not far from the site of the foregoing nest, I saw another young tanager, its dull greenish plumage marked with the earliest flecks of brighter color, helping its parents to attend two nestlings still without expanded feathers. In five hours of the morning it brought food 19 times, while the two parents did so 67 times, so that the young were fed at the rate of 8.6 times per nestling per hour. Eighteen times all the attendants arrived at the nest together, and on 16 of these occasions all three fed the nestlings, leaving only three times when the helper came alone with food. When the trio arrived together, either the helper or one of the parents, whose sexes I could not distinguish, might deliver the food first. Juveniles attending nests also remove fecal sacs. Sometimes, with quivering wings, they solicit food from the parents.

One set of nestlings was brooded by day, in decreasing amounts, until eight days old. When 12 days old they were left exposed at night and during a hard, prolonged afternoon rain. Two other young were alone during the last four of their 15 nights in the nest.

If alarmed by a person coming too near, 12-day-old nestlings flutter to the ground and hop rapidly away, trying to hide beneath the herbage. Two undisturbed siblings left spontaneously when 14 days and a few hours of age. One nestling raised alone also abandoned its nest when about 14 days old, and another solitary nestling did so at slightly less than 15 days. Two siblings also left their nest when 15 days old. At 14 days the fledglings fly fairly well.

LATER BROODS

In the Valley of El General, the over-all breeding season of the Golden-masked Tanager extends from late February to September, an interval long enough for raising three or possibly four broods. Nevertheless, the con-

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centration of laying in the three months of March, April, and May suggests that few, if any pairs continue to nest throughout this long interval; the latest nests probably belong to birds that failed to raise young earlier in the year. My nine records of pairs nesting while accompanied by young in juvenal or early transitional plumage (which sometimes helped them, as earlier told) suggests that second broods are frequent.

In a few instances I learned the interval between two broods. A female, whose two young jumped from the nest somewhat prematurely when 13 days old, laid again in the same nest 12 days later. Another female, whose one surviving young flew from the nest at the age of 15 days, also laid again in the same nest after an interval of 12 days. I do not know whether these three juveniles were still alive when their mothers laid again. Another female relined the nest which her two young left at the age of 15 days and laid in it 23 days after their departure. One of these young tanagers was still nearby. Only two days after their single fledgling left the nest, a different pair started another nest in a neighboring tree. Since this new nest was inaccessible, I could not learn exactly when it received its first egg, but this was probably about nine days after their fledgling left the earlier nest. In other cases the interval between the fledging of one brood and laying in a new nest built near the first one, presumably by the same pair, was much longer, up to 53 days. Possibly, in these cases, the pair had nested somewhere else in the interval. In my earlier account of this tanager (1954) I gave reasons for believing that one pair tried, unsuccessfully, to raise a third brood after having reared at least one young in each of two earlier nests.

The foregoing records refer to true second broods. In view of the high rate of nest failures, replacement nests are probably more frequent than second-brood nests; but I have fewer records of them, possibly because the parents prefer to try again at a greater distance. About 12 days after abandoning, for reasons unknown, a nest with two eggs, a pair started a new nest in the same site, from which I had removed the old nest for study. Another pair began a new nest in a neighboring tree about 17 days after they lost eight-day-old nestlings, and the female laid the first egg of the replacement set 22 days after this loss. This set vanished within two days, and 13 days later the pair started their third nest.

Not only do Golden-masked Tanagers use the same nest twice, of which I have already given several instances, they may even use it three times. Some pairs are strongly attached to a certain site. In mid-May 1943 a pair built a nest 2 m up in a small orange tree, but apparently never laid in it. In March of the following year a new nest was made in this same site, and in it one young was raised. Twelve days after its departure the female laid here the first of two eggs, which vanished a few days later. After remaining empty for 78 days, this already twice-used nest was reconditioned and two more eggs were deposited in it. This time they hatched, but the nestlings promptly disappeared.

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NESTING SUCCESS

My data on the success of 35 nests of known outcome, 21 of which were found not later than the beginning of incubation, are presented in Table 5. By any of the criteria used in the table, the success of Golden-masked Tanagers was much lower than that of Silver-throated Tanagers (Table 4, p. 215), although most of the nests of these related species of similar size were in the same area. The Golden-masked Tanagers' success was also substantially lower than the average for 23 species of birds that build open or roofed nests outside the forest in the same region (Skutch 1966, Table 3). I cannot explain why the Golden-masked Tanager, a widespread, well-established species, had such bad luck with its nests. Possibly the poor success reveals no more than the chances of sampling.

In five of the 25 nests that failed, 10 eggs were inexplicably abandoned. One nest fell with two nestlings. In one nest the single egg was somehow broken. Two nests, in which a total of three eggs were laid, were captured by Blue Tanagers (*Thraupis episcopus*), which deposited their own eggs in them and proceeded to incubate the two kinds together. One of these nests with a mixed set was prematurely destroyed. In the other the Blue Tanagers hatched the Golden-masked Tanagers' egg and raised the nestling along with their own. The young Golden-mask developed more rapidly than its larger nest mates and left the nest first, after which I failed to see it again.

The remaining 16 of the 25 unsuccessful nests were evidently emptied by predators, but in only one case did I witness the act. Early one afternoon, while from the porch I watched Golden-masked parents attend two-week-old nestlings in a calabash tree 15 m distant, a Swallow-tailed Kite (*Elanoides forficatus*) soared high overhead. Suddenly it swooped down, hotly pursued by a Tropical Kingbird (*Tyrannus melancholicus*), and snatched up the nest along with its occupants. Rising high into the air, the kite circled on widespread

TABLE 5
Nesting Success of Golden-masked Tanagers

All nests of known outcome	35
Nests successful (at least 1 young fledged)	10
Nests failed completely	25
Per cent of nests successful	28.6
No. of above nests found before incubation	21
Nests successful (at least 1 young fledged)	5
Nests failed completely	16
Per cent of nests successful	23.8
Eggs laid in 21 nests	40
Eggs hatched	23
Per cent of 40 eggs hatched	57.5
Young fledged from 40 eggs	8
Per cent of 40 eggs producing fledglings	20
Per cent of 23 hatchlings fledged	34.8

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wings, holding the nest in its talons. It bent down its head to extract a nestling, then dropped the nest, which drifted slowly earthward. Returning a few minutes later with food in their bills, the parents found only a bare, mossy crotch where their nest had been. They hunted over surrounding branches and forks, as though searching for the lost nestlings. For the next hour they returned again and again, bringing food for the young that they vainly sought.

PLUMAGE CHANGES

Golden-masked Tanagers leave the nest in a plumage very different from that of adults. The upper parts, from crown to rump, are dull green of varying shades. The remiges are blackish, edged with yellowish green, broadly on the secondaries and more narrowly on the primaries. The tail is black, the breast gray, the abdomen white tinged with buff, and the undertail coverts buff.

A plumage essentially adult is acquired by means of the postjuvenal molt, which is apparently complete. I have detected the first traces of this transformation as early as May, on a young bird that sometimes followed its parents while they attended a later nest. By October most of the young of the year have completed the molt and are difficult to distinguish from adults. However, in early January I noticed a greenish young bird, probably hatched in September in a very late nest, which still followed its parents and was just beginning to acquire the adult plumage. Near Tucurrique, on the Caribbean slope of Costa Rica, I watched a female in a plumage not completely adult attend a nest in June. The black band across her chest was unusually narrow, her remaining underparts were gray rather than white, and her sides and flanks lacked blue.

SUMMARY

Golden-masked Tanagers wander in pairs or family groups through the upper levels of rain forest and into neighboring shady plantations, pastures, and gardens. They eat small fruits, arillate seeds, and insects that they find chiefly on mossy branches and sometimes capture in the air.

Their voice is poorly developed. Their most frequent note, a sharp, dry *tick*, is used in many contexts. Uttered by both sexes, sometimes in a long, rapid series, it serves as a contact note in flight, as an alarm note, and expression of anxiety. Rarely a male has been heard repeating this *tick* over and over at daybreak, as a dawn song devoid of melody.

Generally peaceable birds, Golden-masks rarely fight. In the evening one pair may chase another for many minutes without contact. Such interactions may help to space nests widely.

Although Golden-masks commonly live throughout the year in monogamous pairs, on three occasions trios in full adult plumage attended young. Juveniles more often help their parents to feed younger siblings. A female Tropical Gnatcatcher, which fed Golden-masked nestlings, was tolerated by their parents until she became aggressive toward them.

SCARLET-RUMPED TANAGER

Nests have been found at forest edges but much more frequently in neighboring clearings, and never within closed forest. Most were in mossy crotches of tree or shrub, or amid clustering foliage. A few were inside bunches of green bananas, in old woodpeckers' holes or other cavities in trunks, or in an oropendola's woven pouch. In height, 69 nests ranged from under 2 to about 30 m, with nearly half between 2 and 3.5 m. Both sexes build the compact open cups, coming and going together, the male occasionally feeding his mate. Building usually takes four to six days. Juveniles make gestures of building.

Two eggs are laid early on consecutive days. In the Valley of El General, laying continues from late February to September, but the great majority of sets are laid from March to June.

Only the female incubates, starting after she lays the second egg, and sitting with a constancy of 65 to 75 per cent. Occasionally her mate brings her food. The incubation period is 13 to 15 days.

Both sexes feed the nestlings with insects, spiders, and berries, the male often starting as soon as he sees the hatchlings, an hour or two after they escape from the shells. After brooding ceases the two sexes come and go together, and the male regularly precedes his mate in feeding.

Young in juvenal or transitional plumage not infrequently help their parents to feed subsequent broods and to clean the nests. Their attendance is erratic, spurts of activity alternating with intervals when they bring little food.

Nestlings are brooded by day in decreasing amounts until they are about eight days old. They are left uncovered during their last three or four nights in the nest.

The young leave the nest when they are 14 or 15 days old and can fly fairly well.

Golden-masked Tanagers often try to raise second broods, and sometimes third broods. Intervals between the departure of a brood and the resumption of laying ranged from about nine to 23 days, sometimes longer. The nest is often relined and used for two or even three broods.

Nesting success was poor, only 28.6 per cent of 35 nests found at all stages yielding at least one fledgling. Ten eggs were inexplicably abandoned. Two nests were stolen by Blue Tanagers, which incubated the Golden-masks' eggs along with their own. Others were lost to predators, of which the only one seen in the act was a Swallow-tailed Kite.

Most young Golden-masks acquire adult plumage by means of a postjuvenal molt, between May and October of their first year. One female nested in a plumage not fully adult.

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Ramphocelus passerinii

The longest chapter in the first volume of my *Life Histories of Central American Birds* (1954) deals with this tanager, which was, and remains, the

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most conspicuously abundant nesting bird about my home in the Valley of El General. Here it is represented by the race *R. passerinii costaricensis*, which is confined to the rainy Pacific slope of southern Costa Rica and adjacent Chiriquí, Panama. In their velvety black plumage with vivid scarlet lower back, rump, and upper tail coverts, the males of this form are difficult to distinguish from those of the nominate race, which occurs along the Caribbean side of Middle America from southeastern Mexico to Bocas del Toro, western Panama. Mature females of *costaricensis* are, however, readily distinguishable from those of *passerinii* by their breasts and rumps, which are more or less intense orange, instead of dull yellow or yellowish olive. Otherwise, the females of both races are shades of brown and olive.

Whereas the females of the two forms differ in plumage, the males differ in songfulness, those of the Pacific race being, in my experience, the more persistent songsters, with a somewhat stronger voice. Although certain other tanagers have better voices and more varied songs, none that I know sings more generously than *R. passerinii costaricensis*, which seems to try to compensate for the simplicity of its phrases by repeating them tirelessly, in a pleasant but hardly brilliant voice. Accordingly, I applied the name "Song Tanager" to this race. More recently, I heard, in the Caribbean lowlands of northern Costa Rica, a male of the nominate race whose song was about as sustained as that of the Pacific race, although his voice was weaker.

These tanagers are most abundant in humid regions at low altitudes. The nominate race appears not to extend much above 900 m in northern Central America; but on the Caribbean slope of Costa Rica's Cordillera Central I occasionally met wandering flocks as high as 1,700 m. I found no evidence of nesting at this altitude. On the Pacific slope of southern Costa Rica and adjoining parts of Panama, these tanagers range upward to at least 1,200 m.

Scarlet-rumped Tanagers prefer open country with lush vegetation. In flocks so loose and straggling that it is difficult to ascertain how many birds they contain, but often consisting of about a dozen, they wander through bushy or shady pastures, weedy fields, plantations, gardens rich in shrubbery, riverside or roadside thickets, usually staying rather low. When they venture into more open parts of forest in search of food, they remain well up in the trees, avoiding the dark undergrowth. I have never known these birds to nest even a short distance within closed woodland. Birds in female plumage are considerably more numerous than scarlet-and-black adult males, even at the beginning of the nesting season, when all the males hatched in the preceding year appear to have acquired adult colors.

These tanagers are nervous, suspicious, excitable birds. My earliest attempts to watch them at the nest were repeatedly frustrated by their distrust of a blind that most small birds, even forest-dwellers, soon accepted as part of their inanimate environment. One female abandoned a four-day-old nestling when I left the blind 13 m away. After nesting for years in the shrubbery close around our house, where they are never persecuted by people, although they have other enemies, they have become much less

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timorous, although not really confiding. One cannot approach within meters of an incubating or brooding female without causing her departure from the nest.

These tanagers' temperament is revealed by their behavior at the feeder which, soon after I came to live here, I placed in a guava tree beside the house. They were the first birds to find the bananas that I daily placed upon the board, and they have always been the most frequent attendants. When the chickens discovered that they could fly up to the feeder and devour the birds' fruit, I moved the board to a higher site in a burío tree, about 20 m from its original position. I had hardly descended from the ladder before the tanagers, which had been watching me, flew into the burío tree voicing their nasal note of excitement, a sharp *ac* or *wac*. At first, they looked down at the tempting banana from higher boughs, without daring to approach it. But, after five minutes, a female alighted on the board, bounced up like an elastic ball, dropped and bounced again, and, after coming down the third time, snatched a hasty bite of banana. Soon she gained confidence and ate more freely. Another female, then a male, joined her at the feast. Before long the tanagers were visiting the board frequently. Soon birds of a dozen kinds, from honeycreepers to woodpeckers, were coming in a steady stream.

The situation was quite different when, instead of moving the old board to a new site, I replaced an old, rotting board with bright new wood, which in effect was changing the board's color without altering its location. This was done in mid-morning. Through the remainder of the day, Scarlet-rumped Tanagers came again and again to look down upon the new board and cry out in their usual excitable manner, without once, as far as I saw, alighting upon it to eat banana. Meanwhile, tanagers of four other kinds, and Buff-throated Saltators (*Saltator maximus*), plucked up courage to visit the feeder; but attendance was greatly diminished. On the following morning, while a Speckled Tanager (*Tangara guttata*) ate banana, a male Scarlet-rumped Tanager looked down from above, then descended to the board only to spring up as though it burnt his feet. He dropped down, shot up again, then flew away without having eaten. Presently another male Scarlet-rumped Tanager came to eat and was joined by a female. After this these birds came repeatedly through the day, but in smaller numbers than usual.

Years later when I replaced a rotting, asphalt-coated feeder with a new one that differed chiefly in being shinier black, the Scarlet-rumped Tanagers behaved much the same. For two days they remained aloof, while other birds, chiefly Silver-throated Tanagers (*Tangara icterocephala*) and Blue Honeycreepers (*Cyanerpes cyaneus*) alighted upon the glossy new board. During the following days attendance by all the birds gradually increased.

During the revolution of 1948 I had another exhibition of Scarlet-rumped Tanagers' alert suspiciousness. For some time mercenary troops had been wandering through the valley, plundering, burning, and killing. When we heard that they were approaching our farm, we hurriedly hid as many of our possessions as we could. I threw a pair of new shoes into the midst

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of dense shrubbery, as the quickest way of concealing them. Happily, the pillagers failed to visit us. Before long the excited cries of a crowd of Scarlet-rumped Tanagers drew my attention to the shrubbery, where I expected to find nothing less than a large snake. But the only thing out of the ordinary that I could discover there was a pair of new shoes!

FOOD

These tanagers are versatile foragers. Like other tanagers they are largely frugivorous. Among the fruits that I have seen them eat are guavas; the small black or deep blue berries of *Miconia trinervia* and numerous other shrubs and small trees of the melastome family; the deep purple berries of *Palicourea guianensis*; white berries of the scrambling shrub *Tournefortia bicolor*; and yellow berries of the epiphytic shrub *Lycianthes synanthera*. They join many other birds of the most varied kinds in breaking off and eating fragments from the slender, dangling, green fruiting spikes of the spindling cecropia trees that spring up rapidly in forest clearings. Less frequently they eat the slender green fruiting spikes of one of the shrubby species of *Piper* so abundant in this region, including *P. auritum*. Even before the fruits ripen on tall, spiny pejibaye palms (*Guilielma gasipaes*), Song Tanagers peck into them, although even when ripe these nutritious fruits painfully sting the human mouth unless they are well cooked. They enter more open parts of the forest to peck into bright red fruits of the tall arenilla, a tree of the myrtle family for which I have not succeeded in obtaining an identification.

Many seeds that develop in hard or tough inedible pods are partly or wholly covered by a fleshy outgrowth known as an aril, which is usually rich in oil, poor in starch, and nearly always tasteless or slightly bitter to the human tongue. These arils are often so attractive to birds that they neglect fruits more palatable to us, such as bananas and wild berries, while they eagerly await the dehiscence of the protecting pod and vie with each other for the contents. Scarlet-rumped Tanagers eat arils of *Protium* spp., *Alchornea latifolia*, *Souroubea guianensis*, *Clusia* spp., and *Lacistema aggregatum*. Sometimes they peck into the large, mealy, white aril of a *Protium* seed still attached to the pod and the tree, and sometimes they carry a whole, aril-covered seed away in their bills. The other arillate seeds are small enough to be swallowed whole. After digesting the arils, the birds void the usually indigestible seeds, thereby scattering them widely.

Although the Scarlet-rumped Tanagers' short, thick bills are poorly fitted for drinking nectar, sometimes they try. I have watched them push their heads in among the long, clustered, white stamens of the rose-apple tree (*Eugenia Jambos*), possibly for insects but more probably for nectar. They also probe the much narrower stamen clusters of *Inga* trees, doubtless for the same purpose, and they sip nectar from the clustered white flowers of copalchí (*Croton glabellus*). While Orange-chinned Parakeets (*Brotogeris jugularis*) were plucking and biting the long, slender, red flowers of a poró

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tree (*Erythrina Berteroana*) to extract nectar, a male tanager perched beside a flower and, without plucking it, bit the calyx much as the parakeets did, evidently imitating them. But his bill and tongue were so different from theirs that he probably obtained no nectar, and he did not repeat the attempt.

Scarlet-rumped Tanagers eat the green flowers and tender young fruits of the tacaco (*Polakowskia Tacaco*), a vine of the gourd family sometimes planted for its small, one-seeded fruits, which are tasty when cooked. Probably the tanagers treat the related, more widely planted chayote (*Sechium edule*) in the same way. Buff-throated and Streaked (*Saltator albicollis*) Saltators eat the fruits, flowers, young shoots, and tendrils of both of these vines.

At the feeder these tanagers eat not only bananas and plantains but also oranges that we cut in half transversely and place on the board when bananas are scarce. The number of bananas which they and other birds consume in a day varies inversely with the abundance of wild fruits in the neighborhood. In April and May, when the birds are nesting, and one might expect them to eat more bananas, they take fewer, because arillate seeds and berries, especially those of the abundant trees and shrubs of the melastome family, are available in profusion. After the breeding season the demand for bananas increases and usually remains high throughout the remainder of the rainy season and much of the following dry season.

This species varies its diet with spiders, caterpillars, and winged insects. When, after a shower, the slowly fluttering sexual generation of termites fills the evening air, these tanagers skillfully catch them on the wing. In addition to hunting small creatures amid foliage, they often descend to the ground in grassy places to capture grasshoppers and other invertebrates. When army ants (*Eciton burchelli*) deploy at the woodland's edge or invade the garden, Scarlet-rumped Tanagers join many other birds in snatching up fugitive invertebrates.

Once I watched a female capture a caterpillar that had stripped most of the blade from the midrib of a large leaf at the forest's edge, leaving only enough at the tip to wrap around itself. The tanager found this tight green roll and, hanging back downward from the tip of the dangling leaf, tried to tear it apart. When the bird had exposed enough of the caterpillar, she seized it in her bill and hung suspended below it, tugging at it with all her weight. It had a firm hold on its tube and was not easy to remove. Only on her third attempt did the bird succeed in dislodging the larva by this method. She carried it beyond view.

Very rarely a Scarlet-rumped Tanager captures a small vertebrate, a most unusual food for a tanager. One afternoon when I cleaned out a box of old papers, two pink, naked, recently born mice fell to the ground. After I left a female tanager flew down, took a mouse in her bill, bruised it as well as she could, then carried it to a nestling, which with difficulty gulped down this meal almost as big as itself. Once, through the side window of a blind in which I sat watching an Orange-billed Nightingale-Thrush (*Catharus aurantirostris*), I spied a female Scarlet-rumped Tanager on the ground trying to eat an *Anolis* lizard almost, with its tail, as long as herself.

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The lizard appeared already to be dead; whether she caught it alive, I could not tell. While the tanager struggled, not very successfully, to eat the lizard, another female approached her and she carried it beyond view.

A final item in this tanagers' varied diet is the eggshells of domestic hens, which we throw out to them to replenish their calcium. The tanagers also eat the shells of their own newly hatched eggs.

ROOSTING

In my earlier account I told how Scarlet-rumped Tanagers roosted in a dense hedge of *Stachytarpheta*, a straggling shrub of the verbena family. After this hedge was removed they gathered for the night in a thicket, impenetrable by man, composed of the wiry, tangled, forking fronds of the fern *Dicranopteris* that densely covers a neighboring bank. Here they roost with Black-striped Sparrows (*Arremonops conirostris*). Farther afield these tanagers sleep in tangles of bushes and vines at the forest's edge, or in low, dense thickets. Rarely they roost in a thorny orange tree, with other tanagers that more commonly choose higher roosts.

DISEASES

In past years I sometimes found Scarlet-rumped Tanagers, especially females and young, afflicted by a disease that prevented coordinated movements of the wings. Trying to fly forward, the stricken bird would sometimes land behind its starting point. In severe cases the bird could barely flutter. This disease is not always fatal. After struggling wildly in a tangerine tree, a female fell to the ground and lay quietly, as though dying. I picked her up, finding no external lesions, and put her in a safe place. After about a quarter of an hour she recovered and flew rapidly away. I have not recently found the species so affected, nor have I detected this malady in any other species.

Another disease, which I have noticed chiefly in the wet season, causes the bird's throat to swell out prominently, or internal inflammation that prevents closing of the bill. It also attacks the eyelids, which swell so much that they obstruct vision. Birds nearly blinded by this terrible affliction hang around the feeder all day, as they can hardly find other food. This situation confronts us with a painful dilemma: Should we stop feeding the birds, so that they will disperse and diminish the risk of contagion; or continue to provide food so that the afflicted ones will not starve? The former course, which at the first glimpse appears heartless, seems kinder in the long run, as it probably saves Scarlet-rumped Tanagers and other frugivorous birds from becoming infected. Sometimes, before they finally vanish, the nearly blinded birds become so weak that they are easily caught by hand. We do not try to feed them in confinement, having failed to save chickens similarly affected. Apparently, this disease was brought to El General along with poultry, for I was here nearly two decades before I noticed it. Once it continued to afflict Scarlet-rumped Tanagers for more than two months.

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At least four of those that visited the feeder had bad cases, to which three apparently succumbed. Blue Honeycreepers are susceptible to the same ailment.

SOCIAL RELATIONS

Most Scarlet-rumped Tanagers nest in monogamous pairs, although a few females rear their broods unaided, apparently because there are not enough males to provide partners for all. In the loose flocks that form after the breeding season, pairs are not evident, as they are in the larger flocks of certain parrots and macaws, and among less gregarious tanagers throughout the year. Except in nonpairing birds that form courtship assemblies or leks, courtship displays are rarely seen among constantly resident tropical birds. Pair formation is accomplished so obscurely that it escapes the most zealous watcher, and Scarlet-rumped Tanagers are no exception to this rule. Likewise, coition is rarely witnessed, except among woodpeckers. I have seldom seen it successfully completed, even in a bird so abundant and conspicuous as the Scarlet-rumped Tanager. Evidently it occurs in the privacy of concealing vegetation.

Scarlet-rumped Tanagers do not defend territories. As I earlier told in detail (Skutch, 1954), the posts that males choose for singing at dawn are not related to the sites of the nests that they will attend. These tanagers do not breed in colonies, and usually their nests are rather widely spaced, but I have noticed many exceptions, the extreme case being two active nests only 10 cm apart. Once I watched two females building the same nest with no display of antagonism, while the two males looked on. Later one of these females started a nest slightly over a meter away from the joint undertaking, leaving the other female to finish the latter; but now they pilfered so much from each other's structures that neither could be completed. Meanwhile, a third female, accompanied by a male, stole materials from both of them. All this imbroglio proceeded without fighting by either sex.

Like other nonmigratory members of their family that I know, Scarlet-rumped Tanagers are peaceable birds that rarely engage in conflicts. They do have a threat display, which I have most often witnessed at the feeder. If while one is eating a banana another of either sex alights near it on the board, they may lower their heads and, with slightly open bills, glare at each other across the fruit. This confrontation lasts at most a few seconds, after which they relax and proceed to eat together. Although the board measures only 50 by 30 cm, often six or eight Scarlet-rumped Tanagers are present together, along with other birds. Rarely one tanager, usually a male, tries to keep another off the board, and even more rarely chases the other to a distance, without actual fighting.

One afternoon in March a Buff-throated Saltator stood on the board and thrice drove away a male Scarlet-rumped Tanager that wished to eat there. After the saltator's departure the tanager had his turn. Apparently

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because his agonistic impulses were aroused by the recent encounter, the tanager now tried to drive a Black-striped Sparrow from the table; but the sparrow was insistent and ate opposite the tanager. Although birds of various kinds often repel diners that press them too closely, only exceptionally does one insist upon having the whole board to itself. Such unfriendly behavior continues only while the bird is actually eating. I have never known any bird to try to keep others away when it was not itself eating, as has been reported of certain northern birds.

In my earlier account I wrote that "Song Tanagers are most peaceable birds, never fighting among themselves." This seemed a safe generalization to make after I had lived among them for nearly two decades, but nature has a way of refuting such sweeping generalizations. On 24 March 1954, the day before this statement was published three thousand miles away in Berkeley, California, I witnessed the first fight. Two male Scarlet-rumped Tanagers dropped to the ground from an orange tree beside my study. For a while they lay tightly clinched together. Then they rolled around, clutching and biting one another. After about a minute they separated, and one chased the other through the garden and out over the adjoining pasture until beyond view. I did not learn the cause of this dispute.

Two weeks later, in the same area where the first fight began, one male chased another around and around, continuing this for minutes. Then on 24 April, close in front of the house, I saw two males fall to the ground, clinched together. Here they lay until they noticed me looking down at them, whereupon they separated. Probably the aggressor on all these occasions was the exceptionally zealous male whose mate nested in a *Thunbergia* shrub by the front porch, about 6 meters away from the simultaneously active nest of another pair in a similar shrub. Curiously, I saw no more than one egg in either of these nests. After his mate laid her egg, the zealous male passed a large part of each day in the hibiscus close by her nest, singing or chattering with queer notes. At intervals he went to inspect the nest; once, before the egg hatched, with food in his bill, but concealing foliage prevented my seeing whether he gave it to his mate. Whenever she left the nest he followed her closely and usually escorted her when she returned.

Seven years passed before I again saw Scarlet-rumped Tanagers fight. After grappling on the lawn the two males flew up and perched close together in a nearby bush, where they delayed for about a minute with no sign of enmity. After four more years I watched one male chase another in wide circles through the fruit trees in the pasture. For several minutes the pursuit continued relentlessly; rarely have I seen one bird pursue another so tenaciously. When finally the two tanagers paused for breath in a rose-apple tree, I noticed that the fugitive had a tattered tail, with only three or four feathers left, while the pursuer had a full tail. Soon the pursuit was resumed and continued until the two tanagers flew out of sight.

A little later the male with the tattered tail came to the rose-apple tree with a building female, evidently his mate. Then a male with a whole tail

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arrived in this tree without a mate. Soon afterward three males were involved in a chase, flying one behind another. I could not learn which position Tatter-tail took, or even if he was one of the trio. On the following morning, Tatter-tail continued to escort his building mate to the rose-apple tree. I saw no more pursuits. If his pursuer had tried to take his mate away, the attempt failed.

Another dozen years sped by before I once more saw Scarlet-rumped Tanagers fight. Beneath a tree of *Miconia trinervia* where many birds ate berries, two males grappled one another and rolled around among fallen leaves. After they had struggled in silence for perhaps a minute, one flew beyond view, closely pursued by the other. What an amazing contrast between these strenuous but infrequent struggles and the peaceful tolerance of the three males whose mates were involved in the imbroglio that I watched in the orange tree, and other episodes that I have witnessed! Possibly a mutation, or the introduction of genes from a distant population, has made our local Scarlet-rumped Tanagers more pugnacious than they were when I first studied them. Probably the ability to fight is latent in all birds, if not in all animals, although in many the belligerent impulse is rarely excited.

I have seen female Scarlet-rumped Tanagers grapple even more rarely than males. When an exceptionally bright female gradually dispossessed a duller female from a nest in which the latter incubated two eggs, as told in detail in my earlier account (1954), the intruder won by persistence rather than violence, with much staring at each other. I saw force used only when one bird tried to push the other from the nest's rim. A male looked on without interfering in the conflict. While one female built a nest only 10 cm from that in which another female was incubating, I twice saw them clutch together, but they soon separated to continue their respective tasks.

RELATIONS WITH OTHER ANIMALS

Just as I have rarely seen fighting among Scarlet-rumped Tanagers, so I have seldom seen them contend seriously with other birds. In the few cases that I have witnessed, the other species has usually been the aggressor, as in the tiff between the Buff-throated Saltator and the tanager already recounted. The most violent encounter I ever witnessed at the feeder occurred when a female Scarlet-rumped Tanager alighted on the board where a Black-striped Sparrow was eating. The sparrow lunged at the tanager, making her fly up, then, continuing the attack, darted up beneath her and struck her roundly on the breast with its feet. They promptly separated and went different ways. In a moment the tanager returned to the board and the sparrow flew away.

In an interspecific interaction of a very different sort, a male Blue Honeycreeper repeatedly fed a young Scarlet-rumped Tanager, as I have told in my account of the honeycreeper (1962).

Like most birds, Scarlet-rumped Tanagers try to keep others of all kinds

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from the immediate vicinity of their nests. Even small birds that would not harm eggs or nestlings may, when building, pilfer material from an occupied nest instead of going farther to gather it at its source. A female Variable Seedeater (*Sporophila aurita*) tried to extract pieces from beneath the nest in which a tanager sat incubating two eggs. Aroused by the tugging, the tanager jumped from her nest and drove the intruder away. Most small birds have retreated immediately when threatened by the nest's owner. Often Scarlet-rumped Tanagers are surprisingly tolerant of other birds perching near their nests.

Scarlet-rumped Tanagers with low nests in our dooryard have tried to keep chickens at a distance. Sometimes both parents fluttered close above the heads of an intruding fowl, voicing harsh, nasal cries. One female, whose nest was 1 m up in a *Thunbergia* shrub beside the porch, darted at any chicken that happened to be near as she approached or left her nest. Usually the chickens, including big roosters, squawked and ran away when threatened in this manner, but a hen with chicks refused to be intimidated. As though encouraged by her success, this female tanager formed the habit of menacing chickens on the other side of the lawn, meters away from her nest. She was only bluffing; I never saw her strike one.

Although bold in the face of snakes, Scarlet-rumped Tanagers avoid confrontations with toucans, whose huge, colorful bills serve, among other uses, to intimidate the birds whose eggs and nestlings they devour; so that they are rarely, if ever, attacked by aroused parents while they rest beside a nest in the act of plundering it. Not only do Scarlet-rumped Tanagers flee precipitately from their nests when a Fiery-billed Araçari (*Pteroglossus frantzii*) comes near, I have seen them leave when they heard the calls of these toucans in the distance.

Situated between a large tract of old forest and second-growth woods, our garden is often invaded by snakes, most frequently at the season when nests are most abundant. We are usually made aware of a serpent's arrival by the Scarlet-rumped Tanagers' notes of alarm, which draw birds of other kinds that continue to mob the intruder. One evening in late March the cries of the tanagers nesting close in front of the house made me rush out in time to save newly laid eggs which a yard-long, reddish brown snake was on the point of swallowing. After its removal the tanager settled on her nest. Early in the night she cried out, apparently while sleeping, as she seldom did. I wondered whether birds dream, as horses and dogs seem to do, and whether her recent fright had given her a nightmare.

While I sat at my microscope two days later, harsh scolding drew my attention to a pair of tanagers that was threatening a lance-headed tree snake at the base of a nearby shrub. The snake fled to the neighboring privet hedge, with the tanagers pursuing it closely. After the snake climbed into the hedge, the female tanager approached so near that it struck and apparently hit her. Before I could arrive with a stick, the snake, which resembled a thin brown vine, had vanished. While I searched for it the tanagers did likewise; and, since their eyes were sharper than mine, I waited

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until one of them spied it and started to scold. I struck at it with my machete, but the wiry privet stems protected it. Again the snake disappeared, and again the tanagers revealed its position farther along the hedge. Still shielded by the hedge, it eluded another blow and fled where we could not find it again.

An hour later another alarm among the tanagers called my attention to a long, slender, green tree snake in a calabash tree, over which a vine had grown. The serpent vanished, but half an hour later the tanagers' renewed excitement revealed its presence in another part of the vine. Again the creeper saved it from my blow. On the following day the birds discovered still another kind of snake. No wonder so many of the nests in our garden came to grief!

In June of the same year I had another demonstration of the pertinacity with which Scarlet-rumped Tanagers pursue, and the boldness of their attacks upon, the chief despoilers of their nests. The rasping notes of a female revealed the presence of a four-foot green tree snake in the broad, leafy crown of the mango tree beside my study, where she had a nest with two eggs, so well hidden amid clustering foliage that I had not previously discovered it. My efforts to knock the snake down with a long pole failed, but the tanager continued to harass it until it fell to the ground. It reached the hedge and vanished before I could catch it. For the next few hours the complaints and scolds of the tanagers, renewed from time to time, distracted me from my writing. At noon I found them and other small birds flitting excitedly about the snake high in the guava tree that supported the feeder. A female Scarlet-rumped Tanager twice nipped the serpent's tail, while it drew back its head with widely distended mouth, as though to strike. Again it escaped when I tried to reach it with a long pole. But the birds did not forget it, nor permit me to do so. Finally they traced it to an orange tree, where I killed it to save their nests and restore tranquility to our dooryard.

The foolish destruction, by the local people, of Laughing Falcons (*Herpetotheres cachinnans*) and other animals that habitually or occasionally eat snakes seems to have permitted their increase. In some years snakes, chiefly nonvenomous kinds, have been a plague around our house. Despite the tales that one hears about snakes' "charming" and catching birds, and despite all the attacks I have seen by sparrow-sized passerine birds of various families upon snakes very much bigger than themselves, I have only once known a snake to seize a fully fledged bird. One morning in May, while I sat writing, agonized cries caused me to look up. In the croton shrub in front of my door, where a Scarlet-rumped Tanager had a nest with one egg, I beheld her dangling and fluttering wildly, with one wing held in the jaws of a green tree snake. Although the serpent was a meter long, it was hardly thicker than my middle finger, and I doubted that it could swallow the bird. Sympathy overcoming scientific curiosity, I did not wait to observe the outcome of this encounter, but seized the first stick I could lay hands on and freed the tanager. Probably she had boldly attacked the snake to

save her nest, to which she soon returned. Similar courage in repelling a snake from their nest was reported by Pettingill (1976) of a pair of Veeries (*Catharus fuscescens*).

I have never seen a Scarlet-rumped Tanager give a distraction display. Indeed, I have never seen any species of tanager "feign injury" convincingly.

One afternoon in April, on the lawn beneath the spreading mango tree, I watched a female Scarlet-rumped Tanager attack a mantis. The green insect stood upright on its middle and hind legs, holding its forelegs, which were separated from the former by nearly the whole length of its long, thin thorax, widely spread and rising somewhat above the level of its head. At the same time, it spread its short, broad wings sideward. Each green forewing bore in the middle a nearly round, dull red spot, with an elongated black mark at the center and some yellow around the edge, the whole forming a crude eye-spot. The transparent, colorless, pleated hindwings were boldly marked with narrow, transverse, yellow bands. In this menacing attitude, displaying these strikingly colored wings, the mantis confronted the tanager, waving its arms toward her. Uttering calls of alarm, the bird approached close to the insect but apparently did not touch it. Presently she flew off, but soon returned to be greeted by the same threatening arms. With another cry of alarm, the tanager again retreated. Then I picked up the insect uninjured. It was 6 cm long, its anterior wings 3 cm long by 1 cm broad, and it would have made a substantial meal for a bird bold enough to seize it.

In May, some years later, I saw a large, green longhorn grasshopper or locust fly low across a pasture, closely pursued by a male and a female Scarlet-rumped Tanager. The insect alighted among low herbs, while the birds continued beyond it. Soon the male tanager returned to the orthopteron, which had climbed up a sprout about 30 cm high. Whenever the bird attacked, the insect spread its dark brown, green-margined underwings and violently shook itself along with its support. After a few feints of attack, the tanager withdrew, leaving the locust unharmed. The insect behaved the same way when I touched it. These episodes demonstrated the value of the markings and ruses by which insects that are evidently palatable save themselves from being devoured, even when assailed by birds bold enough to attack snakes very much bigger and more dangerous than the insects. But why are the tanagers so much more timid in the presence of the insect than in the presence of the reptile? Doubtless, it is because the loss of a meal, when food is abundant, is far less serious than the loss of eggs or young.

Usually when a party of tanagers continues to raise cries of alarm, the cause of their excitement is a snake. Sometimes, however, it is nothing more formidable than an exceptionally large moth, perhaps bedraggled and moribund after the drenching rains of the preceding afternoon and night, slowly waving its wide, dark wings as it dies. The Scarlet-rumped Tanagers' calls draw a variety of other small birds, including other kinds of tanagers, finches, honeycreepers, warblers, wrens, flycatchers, hummingbirds, and sometimes an antbird from the neighboring forest, all of which

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flit around and complain, forming a typical "mobbing" party. They do not attack the moth, which apparently they have no desire to eat. Each movement of the sluggish insect causes a fresh spasm of excitement among the surrounding birds. After a while the party dissolves, leaving the moth to expire in peace; but if a passing Scarlet-rumped Tanager notices it again, the bird's loud calls may attract another group of mobbers. This is strange behavior by birds that certainly must be familiar with the abundant, large, harmless moths of the tropics; but what can one expect of birds that will mob a pair of shoes?

NEST

About the time that male Scarlet-rumped Tanagers start to sing, and rarely more than a week later, females begin to build their nests. In 1943 I recorded the year's first sustained song, and found the first female building, on 26 February. Although females and even males may pick up material, only to drop it, considerably earlier, the earliest date at which I have noticed building was 19 February 1959. In 1958 I saw a female start a nest on 21 February; and in four other years (1946, 1961, 1962, and 1970) nest construction had begun by 22 February. Both singing and nesting are likely to start considerably earlier when the dry season is relieved by occasional showers, or when the rainy season sets in early, than when the dry season is severe and prolonged. In many years I have heard little song, and noticed no nesting activity, until March. If the weather becomes dry after a nest is started, building may take substantially longer than at the height of the nesting season, or it may be discontinued.

Although I earlier (1954) wrote that the female Scarlet-rumped Tanager apparently chooses the nest site without the assistance of the male, I have since seen exceptions to this. At the beginning of April 1957, a male repeatedly visited a shrub of *Thunbergia erecta* in front of my study window and sang. After this behavior had continued for several days, his mate came repeatedly to this shrub and rested in the same place amid close-set twigs near the top, usually while the male perched, often singing, below her in the bush. On the following day, the female started to build in the site that she had repeatedly tested. After four days of unhurried building the nest was finished, and two days later an egg was laid. In late March of the following year a pair of tanagers, probably the same, flew into this *Thunbergia* and stayed together, as though examining a nest site. On the following morning the male entered this shrub and sang loudly for a good while. There was still no trace of a nest, but in the afternoon the female started to build in this site. Again that afternoon the male sang for about one minute in the center of the low, densely branched shrub. Soon afterward the female brought another billful of material, but she did not continue to build. Two years later I saw a pair prospecting for a nest site in a different *Thunbergia*, where a nest was completed and eggs laid. The more attentive males take great interest in the female's selection of a nest site and apparently may

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influence her choice. One male came repeatedly to sing close beside a nest from which two young had fledged three weeks earlier, as though trying to induce his mate to lay there again. For over a month after the young left another nest, their male parent came almost daily, sometimes twice, to sing profusely while standing in the empty nest, on its rim, or close beside it. Finally, 46 days after the young flew, another nest was started a few meters from the site of the first.

The nests that I have seen were in dooryard shrubbery, fruit trees, bushy pastures, or fields overgrown with tall, coarse weeds, never in old forest or even tall second-growth woods with a nearly closed canopy. In our garden the crowded, thin, densely leafy, upright stems of pruned shrubs of *Thunbergia erecta* are favorite sites. Many nests are built amid the large, broad, clustered, red-and-green leaves of the caña de India (*Taetsia terminalis* var. *ferrea*). Thorny, full-foliaged orange trees are often chosen. Almost any shrub, small tree, or vine tangle that offers support and a measure of concealment is an acceptable site. Although the open branches of cordoncillo (*Piper* spp.) give poor concealment, these shrubs are sometimes used, probably because this huge genus is so abundant. Even stout grasses, such as sugarcane, maize, or Guinea grass, and ferns like the bracken (*Pteridium*) occasionally support a Scarlet-rumped Tanager's nest. Those of which I have recorded the height were situated as follows:

under 1.2 m:	35 nests
1.2 to 2.5 m	135 nests
2.5 to 3.7 m	43 nests
3.7 to 5 m	23 nests
5 m to 6 m	15 nests
over 6 m	<u>1 nests</u>
Total	252 nests

Well over half the nests were 1.2 to 2.5 m above the ground. The two lowest were only 36 cm up. The highest was 6.4 m up in a mango tree. The attraction of the highest sites appears to be exceptionally good concealment by the compact crown of a low tree. The highest nests are hidden better than most, and it is often difficult to see their contents amid clustered foliage. Two Scarlet-rumped Tanagers occasionally build close together. One made her nest only 10 cm from an incubating female. Five other active nests were separated by .6, .9, .9, 1.5, 1.5 m. Another five nests were 1.8 to 3.0 m apart. The great majority of nests are more widely separated.

Although a male tanager sometimes plucks fragments of vegetation only to drop them, I have never seen one help his building mate. Often he follows her as she gathers materials and brings them to the nest, then perches nearby and sings or chatters with squeaky notes while she deposits it and vigorously shapes the growing structure. Although, like most birds, these tanagers build most actively in the early forenoon, sometimes they work

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hard in the hot sunshine between one and two o'clock of the afternoon. In the first six hours of the day one female made 87 trips to her nest, on most, if not all, bringing contributions. Between 9:00 and 10:00 she came 24 times, the most active building that I have recorded. Although the earliest nests may not be finished until a week or two after they were started, later most nests are built in from three to five or six days.

The completed nest is a substantial open cup, measuring 10 to 13 cm in external diameter by 6.5 to 8 cm high. The interior is about 8 cm wide by 4.5 to 5 cm deep. The bulk of the nest usually consists of dry leaves, often strips of large monocotyledonous leaves, such as those of the banana, wild plantain (*Heliconia* spp.), shellflower (*Calathea* spp.), or canna. Some of these pieces are 5 or even 8 cm wide. If these large herbaceous plants are not available, the narrower blades of grasses may be used. The flat pieces are held together by an outer network of cordlike or fibrous materials, much of which is also placed between the layers of leaves. This binding material may include thin, dry herbaceous vines, weed stems, wiry roots, bast fibers, horsehairs, or hairlike fungal rhizomorphs. The often thin inner lining is composed of some of the finer of these materials.

Sometimes the outside of the nest is adorned with a spray or two of living fern, such as a small-leaved, wiry-stemmed polypody (often *Polypodium ciliatum*) that creeps over trunks and branches, or with fragments of the larger fronds of *Nephrolepis* or some other fern. In my experience, the nominate race of the Scarlet-rumped Tanager, on the wetter Caribbean side of Central America, more consistently ornaments its nest with a touch of green. This tanager does not often include down in its nests, but one female, building near a balsa tree (*Ochroma* sp.) that was shedding great fluffs of the softest seed down, could not resist bringing so much of it to her nest that I could not imagine which the builder was until I saw her. Often the tanager flies afar seeking these diverse ingredients.

EGGS

In seven nests the first egg was laid on the morning after building stopped. At nine nests the female permitted a day to elapse between the completion of her work and the deposition of her first egg, which was, accordingly, laid on the second morning after building ceased. In four cases the nest remained empty for 3 nights and 2 days before the female laid; and in two others it did so for 4 nights and 3 days. In one of the earliest nests the interval was 5 nights and 4 days. The interval from the beginning of construction to the start of laying was in one case 4 days; in seven 5 days; in eight 6 days; in one 7 days; in two 8 days; in one 13 days; in one 15 days; and in one 19 days. All the intervals of more than 6 days were for nests started in late February or early March. However, a nest begun on 24 February 1961 received its first egg on 1 March, 5 days later.

The two eggs of the normal set are laid early on consecutive days, from a little before to shortly after sunrise. I have not determined the precise

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hour of laying, but in 50 cases I have bracketed it between two visits to the nest. No egg was laid before 5:15, and none later than 6:55. Four eggs were laid before 5:50; 26 before 6:15; 39 before 6:30. Only three eggs are definitely known to have been laid after 6:00. Probably most eggs were laid between 5:30 and 6:15, although I did not see them until I inspected the nest at about 6:30 or a little later. One female laid her second egg while sitting in the nest from 5:35 to 6:14; another from 5:47 to 6:22; a third from 5:50 to 6:42. Although some finches and other birds lay their second egg considerably later in the morning than they lay their first, this is not true of this tanager (Skutch, 1976). I have noticed no consistent difference between the time of laying of their first and second eggs. Often the male escorts the female to the nest when she comes to lay.

Of the 246 nests in which I have recorded what appeared to be the full complement of eggs or nestlings, 225 contained 2 eggs. Each of four nests held 3 eggs. One of these sets of 3 was definitely the product of two females, the second of which wrested the nest away from the first after the latter had laid 2 eggs, as already told. Possibly an egg was lost in the contest for possession of the nest. The other three sets of 3 eggs were all laid in our garden in 1946, 1947, and 1949. Each set was fairly uniform in size and coloration. In two of these sets all three eggs hatched on the same morning; in the third set one egg hatched more than a day after the other two. I never saw more than one female attending any of these three nests and have no doubt that each set of three was laid by a single female; most probably all three sets by the same prolific bird. The single four-egg nest took so long to build that I lost interest in it. Returning after an interval, I was surprised to find four eggs, which were readily separable into two pairs that differed conspicuously in size and shape, although not in color. I watched this nest continuously for four hours without seeing a second female, or any male, show interest in it; probably it changed ownership like the first of the nests with three eggs. Unfortunately, all the eggs vanished before I could make further studies.

Excluding one-egg nests that I visited only once and could not be certain that another egg was not laid later, I have records of 16 nests with a solitary egg. The interpretation of these records is made difficult by heavy predation. Early on 22 May 1978 a female laid her first egg in a nest in a shrub in front of our house. By noon this egg had been swallowed by a green tree snake, which we found at the nest and killed. On the following morning the tanager laid her second egg in the empty nest, where she successfully raised her nestling. If I had not discovered the snake, or had not inspected the nest between the laying of the first and second eggs, I might have mistaken the second egg for the first and concluded that this was a one-egg nest.

In three other cases in which the first egg vanished less than 24 hours after it was laid, second eggs were not laid in the ravaged nests. I failed to learn what the tanagers did with them. In the dusk of 20 April 1944 I watched the female go to Nest 81, as though to sleep on her newly laid

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first egg; the following day her nest was empty. In view of these uncertainties, I cannot be sure that, without interference, a Scarlet-rumped Tanager ever incubates a single egg. However, I think it probable that she sometimes does so at the beginning of the breeding season, in March, when four of the one-egg nests were found, and at the end of the season, in July, when I discovered two such nests. Thus, in March 1948, a very dry year, when several females started nests that they did not finish, one completed a nest in which I never saw more than one egg.

The eggs vary in both shape and color. Even in a set of two they sometimes differ so much that it is hard to believe that they were laid by the same bird. They may be long- or short-ovate. The ground color ranges from pale blue to blue-gray, pale gray, or almost white, with no trace of blue. The eggs are marked with large and small blotches, fine dots, and scrawls of black, brown of varying shades, and pale lilac. These markings are often very irregular in shape and usually heaviest and most crowded in a wreath around the egg's thicker end, with a light scattering over the remaining surface. On some eggs the brown spots predominate; on others the black, with at times no brown at all. Fifty eggs measured at the nest averaged 23.7 by 17.0 mm. The eggs showing the four extremes measured 27.8 by 16.7, 21.4 by 16.3, 23.8 by 18.3, and 21.4 by 15.9 mm. The weights of six fresh eggs ranged from 3.1 to 4.0 g, with an average of 3.65 g.

In 267 nests in the Valley of El General from 1936 to 1979, eggs were laid as follows: March, 72; April, 80; May, 72; June, 26; July, 11; August, 5; September, 1. The earliest of these eggs were laid on 1 March in 1961 and 1964. A full-grown young bird that was fed by his father through the first week of December 1957 might have been hatched from an egg laid in October.

INCUBATION

Only the female Scarlet-rumped Tanager incubates. On the day when she lays her first egg she sits upon it for brief periods. Often, perhaps usually, she sleeps on her single egg before laying the second next morning. I have six records of females passing the night on the first egg, and three records of their absence. Because they are so easily frightened from the nest, I have made few observations on this point. These differences in the females' behavior are reflected in the hatching of the two eggs, which at some nests is spread more widely than at others.

Some females reach full incubation constancy sooner than others. During the same four hours of watching on each day, the female of Nest 65 incubated 11.3 per cent of the time on the day she laid her first egg, 30.0 per cent on the day she laid her second egg, 54.6 per cent on the following day, and 66.7 per cent four days later. On the day another female laid her second egg, she incubated for 60 per cent of the same four hours. A third female incubated for 59.1 per cent of these hours on the day she laid her second egg.

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After they reached full constancy, three females, that I watched for a total of 33 hours, incubated for 71.2, 74.3, and 75.3 per cent of the observation periods. A fourth, which after each brief absence hurried back to her nest because another Scarlet-rumped Tanager was building only 10 cm away, sat for 84.5 per cent of six hours—exceptionally high constancy for this species. The sessions of these four tanagers ranged from 6 to more than 104 minutes, with averages of 29.3, 33.6, 34.5, and 28.3 minutes. Their recesses fluctuated from 1 to 32 minutes, with averages of 11.8, 11.6, 11.3, and 5.2 minutes—the last by the female which sat with highest constancy. By far the longest sessions that I recorded—all that exceeded one hour—were in the middle of the day, when the incubating female appeared to take a “siesta” on her nest; although, as far as I saw, she did not sleep with closed eyes. At the same time, other tanagers, that were not feeding nestlings, were rarely seen and appeared to be resting amid concealing foliage. Incubating birds of other species that I have watched have not taken exceptionally long sessions around noon.

Some female Scarlet-rumped Tanagers nest without an attendant male. Most, however, are regularly mated and their partners escort them on at least some of their returns to the nest, although not as consistently as do males of tanagers that live in obvious pairs throughout the year, especially species of *Tangara*. Male Scarlet-rumped Tanagers tend to be most attentive during nest building, laying, the beginning of incubation, and when the eggs are about to hatch, rather than through most of the incubation period. Few keep such close watch over the nest as did the exceptionally zealous male of which I earlier wrote. From time to time a male approaches a nest with food in his bill and, lowering his head into the bowl and uttering queer low sounds, appears to offer it to the eggs—anticipating their hatching, as I have seen in a number of other birds (Skutch, 1976). Even if the female happens to be present when her mate brings food for the eggs, she does not accept it. Nuptial feeding, so widespread among tanagers, has not been observed in this species. More rarely the female brings food before her eggs hatch. Two days before she laid her first egg, one female came at noon with food in her bill, perched on the rim, lowered her head, and uttered chirping notes, as though coaxing nestlings to take a meal. Then she sat in the eggless nest.

HATCHING AND INCUBATION PERIOD

At most nests, on the eleventh day after the second egg was laid, one can detect with a fingertip a slight roughness at a single point on or near the greatest transverse diameter of the eggs—the first indication that they will soon hatch. From about 16 to 25 hours after an egg is pipped, it hatches. By far the greater part of this interval is occupied by the effort to pierce the shell. After the hatchling has made an opening into which it can stick its bill, it extends the gap laterally, and soon pushes off the shell's thick end as a neat cap. Then it wriggles out into the nest, its sparse,

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wet down plastered against its pink skin in thick, curly strands. The empty shell is promptly eaten by its mother.

In 33 nests the second egg, and usually both eggs, hatched on the twelfth day after the set was completed. In six nests the eggs hatched on the thirteenth day; in one on the fourteenth; and in one on the fifteenth day. Some of the nests where incubation was prolonged beyond the twelfth day were subject to frequent disturbance, for the female left her eggs whenever a human passed by, which, in nests close to houses or paths, was frequent. The eggs that took 15 days to hatch were in a shrub near the kitchen door where human activity was great. Even nestlings that took so long to hatch developed normally and fledged at the usual age of 12 days.

At a number of nests I tried to determine the incubation period more precisely, by bracketing the times of laying and hatching as closely as possible without excessive disturbance. Many of the eggs of which I timed the laying were prematurely lost, but in 17 nests they survived to hatch. No second egg hatched in less than 11 days 23-1/2 hours after it was laid. The longest possible period at one nest, where the second egg hatched at 7:25, was 12 days 2 hours. In only two of the 16 nests in which the eggs hatched on the twelfth day could the incubation period have been as long as 12 days 12 hours. The average of the shortest possible periods was 12 days 4.27 hours, and that of the longest possible periods 12 days 7.39 hours. The mean between these averages is 12 days plus 5.83 hours, or approximately a quarter of a day. Thus, 12-1/4 days is about as accurate as it is practicable to determine the average duration of incubation at relatively undisturbed nests of the Scarlet-rumped Tanager. My most accurate determination of the incubation period of the nominate race, *R. p. passerinii*, was also 12-1/4 days.

Eggs may hatch even after a night's exposure to rain far along in the incubation period. Two first nestlings hatched in the night, 16 in the forenoon, and one in the afternoon. Of 28 second nestlings, 1 hatched in the night, 14 in the forenoon, 2 around midday, and 11 in the afternoon. In a few nests where I marked the eggs, all but one hatched in the order in which they were laid. Evidently the first egg usually hatches several hours before the second because the female covers it briefly on the day it is laid and often through the following night, before she lays the second egg.

In some birds a diurnal periodicity of hatching has been observed. In certain passerines most eggs hatch in the night (probably toward its end) or in the forenoon; few in the afternoon (Skutch, 1952, 1976). Two explanations of this periodicity deserve consideration. The activity of the hatchling, like that of many adult birds, may be greatest in the morning, because through the night it has been warmed continuously, rather than intermittently as during the day, or because the light that penetrates its shell has induced a diurnal periodicity in its efforts to escape. On the other hand, if eggs are laid at a definite hour, and embryonic development proceeds at about the same rate in all the eggs of a species, the chicks should all be ready to hatch at about the same hour. The first explanation may well

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apply to the first-laid eggs of Scarlet-rumped Tanager's sets of two, which, despite the varying amounts of incubation they receive before the second eggs are laid, usually hatch in the forenoon. Second eggs may often fail to hatch before midday because they are laid early in the morning and the chick's development to the point of emergence takes, on the average, 12-1/4 days, with the result that those which develop somewhat more slowly are not ready to hatch before noon on their twelfth day, and they do not wait until the following morning.

NESTLINGS

Development.—The newly hatched Scarlet-rumped Tanager is a typical passerine nestling, with sparse gray down shading but by no means covering its pink skin. Its eyes are tightly closed. The interior of its mouth is red, sometimes becoming paler or more orange toward the center, and the prominent oral flanges are white. On the roof of the mouth and rear edge of the expanded anterior part of the tongue are bristlelike, downward or inwardly directed projections, hard to see without a magnifying glass, which evidently serve to keep food placed in the mouth by the parents from slipping out. The egg tooth is a minute, light-colored projection, also difficult to distinguish without magnification, on the culmen of the upper mandible, just behind the tip. Two nestlings, from eggs that weighed 3.7 when fresh and 3.2 when on the point of hatching, each weighted 3.1 g after they dried.

By the third day after they hatched, the nestlings' eyelids began to open and the pins of the remiges were becoming prominent. At this age one uttered a weak *peep* when lifted from the nest—the first sound that I heard from a nestling.

By the fifth day the eyes could be opened, the pins of the remiges and their greater coverts were conspicuously long, and the body feathers were sprouting. The interior of the mouth had become redder.

On the sixth day open-eyed nestlings still gaped when I held a hand above them. One cried out when lifted. One tried to perch on the edge of the little box in which it was placed for weighing. All the feathers were still ensheathed.

On the seventh day both nestlings gaped to my hand. The remiges and some body feathers were pushing out from the tips of their sheaths, but the less developed head feathers and rectrices were still enclosed.

On their eighth day the nestlings crouched instead of gaping when I moved a hand over the nest, and one cried out in alarm. When held in my hand, one gaped, while the other crouched and gave cries of alarm. The body feathers were quite generally escaping from their sheaths.

When nine days old the nestlings were rapidly becoming feathered. They crouched low in the nest when I approached.

By the twelfth day after hatching the nestlings were well feathered, although with rudimentary tails, and ready to leave the nest. They could fly weakly.

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The egg tooth, instead of falling, as on some chicks, remained as a minute projection near the tip of the culmen, visible with a magnifier.

Brooding.—All brooding is done by the female. A bird with newly hatched nestlings broods them almost as constantly as she had incubated. Four females brooded, respectively, 60.3, 72.1, 71.3, and 61.6 per cent of the morning on which their first nestling hatched, which is only slightly less than the 71.2 to 75.3 per cent constancy that I found during incubation at three nests. At two nests the females remained sitting for the exceptionally long intervals of 50 and 55 minutes while the first egg was hatching beneath them—only when taking the midday “siesta,” and while rain falls, do these tanagers ordinarily remain sitting as long as this in the daytime. But two other females sat more briefly, for 32 and 35 minutes, while the first egg was hatching. While the hatchling emerges from the egg beneath her, the parent sits restlessly, continuing this until she picks up a piece of the empty shell, crushes it in her thick blue bill, and eats it. The other part of the neatly divided shell promptly follows the first. After the nestlings have escaped the shell and need food, both the sessions of brooding and absences from the nest tend to become shorter, and also more variable, than during incubation of the eggs. This is especially true if the female leaves the nest whenever her mate brings food, instead of continuing to sit and taking it from him for delivery to the nestlings.

In fair weather the amount of daytime brooding declines rapidly from day to day. When five days old and bristling with pinfeathers but still without expanded plumage, the nestlings are rarely brooded as long as 10 minutes. By the sixth or seventh day they are seldom brooded in fair, warm weather. But while rain falls, their mother covers them almost continuously. Even after the young are well feathered their mother hurries to the nest when a hard shower begins, and often she stays there until it stops. She broods them during their next-to-last and often also through their final night in the nest. The mother of the unusually large brood of three brooded the third nestling in the night after the other two had left. Another female slept on the rim of the nest beside her 11-day-old nestlings, with her tail above them, her head turned back and hidden in her feathers.

Feeding.—As far as I have seen, the female Scarlet-rumped Tanager always eats the empty shell, thereby assuring one who watches from a blind that an egg has just hatched. At four nests she brought the first meal to her first nestling 29, 36, 38, and 64 minutes after this act. Five males took longer to begin feeding: 38 minutes, 92 minutes, 4 hours and 49 minutes, at least 14 hours, and slightly over 24 hours; but the last two intervals include 11 hours of darkness and inactivity. As a rule, the male parent starts to feed the nestlings on the day they hatch, except at a small minority of nests where the female appears to lack a mate.

At four of the five nests that I watched most carefully during hatching, the male first saw his offspring when he arrived with food for them. Did he know that they had hatched before he saw them and, if so, how did

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he learn? One's first surmise would be that his mate informed him that he had become a father with work to do, but I do not believe that this is correct. If she can break the news to him, why does he sometimes delay so long to begin his paternal task? Careful watching at the nests of many species of birds has failed to convince me that the female parent, or whichever is in charge when the first egg hatches, ever informs the partner, as by a special note or gesture, that a nestling has arrived (Skutch, 1976).

As we have learned, the male Scarlet-rumped Tanager occasionally brings food to a nest with intact eggs, anticipating their hatching. When he does not feed the nestlings until many hours after their birth, it seems likely that he has come on another of his anticipatory visits, and now at last happens to find a mouth or two to receive his offering. Since his anticipatory visits are nearly always widely spaced, it is improbable, but of course not impossible, that one will come only an hour or two after the nestlings hatch. The most probable explanation of such prompt feeding is that the male was incited to bring food by seeing his mate carry or deliver it.

Although these tanagers are largely frugivorous, their nestlings' diet consists chiefly of insects, including small green grasshoppers that they catch in the grass. Often the parent so mangles them before bringing them to the nest that identification is difficult. Nevertheless, parents often deliver large insects without removing the wings, which the nestlings gulp down whole. Several items may be brought on a single visit, perhaps one held prominently in the bill and the rest in the mouth or throat, or else all hidden inside. Very rarely a nestling receives a vertebrate, such as a tiny lizard or a baby mouse. Fruit, including banana from the feeder, varies the diet, especially as the nestlings grow older.

At some nests the male delivers food to the female if he finds her brooding, and she rises up to pass it to the nestlings beneath her. Other pairs do not learn to cooperate so closely; when the male arrives the female leaves the nest, even in the rain, so that he may feed the young directly. When the male of a pair that nested beside our porch came in the rain with food, his mate was sometimes slow to leave. He would perch below the nest, singing sweetly despite his full mouth, until she uncovered the nest and he could feed the nestlings. Then she promptly returned to shield them from the rain. Both parents coax newly hatched nestlings long and patiently to take their food, offering it again and again, sometimes pressing it in the mandibles between presentations, meanwhile voicing sharp or squeaky notes, until finally it is swallowed, or the parent abandons the attempt to deliver it. Sometimes such coaxing continues for five or six minutes. Older nestlings usually stretch up their gaping red mouths as soon as a parent arrives, and rarely need to be alerted by sharp notes.

Table 6 gives the rates of feeding at 14 nests of the Pacific race of the Scarlet-rumped Tanager and, for comparison, at one nest of the nominate race, at two nests of a single pair of Crimson-backed Tanagers (*Ramphocelus dimidiatus*) in Panama, and at a nest of the Silver-beaked Tanager (*R. carbo*) in Venezuela. At all these nests, except that of the Crimson-backed Tanager,

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the male, even when present, brought food less frequently, often much less frequently, than the female. At two Scarlet-rumped Tanagers' nests that appear in the table, and at three others so near my dwelling that they were often watched, although not for long intervals, no male was in attendance; and the same was true of the Silver-beak's nest beside the house we occupied in northern Venezuela. From the table it appears that females compensate for the lax attendance, or complete absence, of a male.

Table 6 also shows how the rate of feeding is adjusted to the number of nestlings. Each nestling of the exceptional brood of three in Nest 124 was fed nearly as often as each member of the normal brood of two, at

TABLE 6
Rates of Feeding Nestlings in the Genus *Ramphocelus*

Species		No. of nestlings	Age of nestlings in days	Hours watched	Number of feedings			Feedings per hour per nestling
					Male	Female	Total	
Scarlet-rumped Tanager, <i>R.p. costaricensis</i>								
Nest	4	2	4-5	2	6	12	18	4.5
	4	2	10-11	1.5	6	11	17	5.7
	19	2	10	2	10	16	26	6.5
	30	2	ca 7	2	8	15	23	5.8
	37	1	ca 7	2	0	9	9	4.5
	37	1	ca 12	1	0	13	13	13.0
	49	2	ca 9	3	14	17	31	5.2
	52	2	ca 6	2	16	17	33	8.3
	53	2	10-11	2	7	20	27	6.8
	89	2	5-7	12	56	93	149	6.2
	89	2	11	5	22	37	59	5.9
	121	1	10	5	0	42	42	8.4
	124	3	11	5	40	46	86	5.7
	135	3	3-5	3	8	10	18	2.0
	151	2	6	5	9	66	75	7.5
	151 ¹	3	5-7	5	23	83	106	7.1
	151 ²	1	8	5	8	28	36	7.2
	167	3	10-11	12	74	137	211	5.8
	169	2	7-8	12	45	128	173	7.2
<i>R.p. passerinii</i>		2	9-12	4	3	25	28	3.5
Crimson-backed Tanager, <i>R. dimidiatus</i>								
		2	6	3	6	13	19	3.2
		2	3	3	10	4	14	2.3
		2	9-10	4	10	10	20	2.5
Silver-beaked Tanager, <i>R. carbo</i>								
		1	6	4	0	21	21	5.3

¹ A five-day-old nestling from another nest was temporarily placed in Nest 151.

² A nestling from Nest 151 was temporarily placed in another nest.

the same age, in Nest 89. The single ten-day-old nestling in Nest 121, although attended by its mother alone, was fed much more frequently than each nestling of most broods of two, which is in conformity with Moreau's (1939, 1940, 1947) studies at nests of a number of African birds, although he found exceptions to this rule.

In May 1948 I had, close by the house, two Scarlet-rumped Tanagers' nests, each with two nestlings, those in one nest only two days older than those in the other. In order to learn how the parents would adjust to changes in brood size, I spent a morning counting feedings at Nest 151, while it held its proper brood of two. That evening I added to this nest one nestling from the neighboring nest, and the following morning I again made a record of activities. In the afternoon of that day I returned the borrowed nestling to its own parents, and in the evening I gave them, temporarily, one nestling from Nest 151. Then, next morning, I watched this nest while it had a single nestling. The parents, especially the female, adjusted their rate of feeding surprisingly well to the number of mouths they had to fill. The single nestling was fed at the rate of 7.2 times per hour; two nestlings, 7.5 times each; and the trio at the rate of 7.1 times per nestling hour (Table 6). The single nestling made hardly any sound at mealtime, in sharp contrast to the loud peeping of the trio. Evidently these cries stimulated the parents to bring food more often, especially the male, which nearly trebled his rate of feeding when the third nestling was added to his brood. These observations support the conclusion of Haartman (1953) that the clamor of the hungriest nestling(s) determines the rate of feeding.

On the morning when Nest 151 held two nestlings, the female first brought food at 5:33, and before she resumed brooding at 6:04 she had fed the nestlings 12 times. The male did not feed the two until 8:00, and in the next half hour did so five times—more than half his morning's contribution. On the dark and misty morning when Nest 151 held three nestlings, the female brought the first meal at 5:39, and fed 10 times before she resumed brooding at 5:59. The male first brought food to the trio at 5:59, two hours earlier than on the preceding day when only two nestlings were present. On the following day the female started to feed the single nestling at 5:34, and had fed it six times when she resumed brooding at 6:12 on this exceptionally chilly morning. Her mate, perhaps expecting the large brood that was present on the preceding day, brought his first contribution at 5:50.

Although, as at Nest 151, the nestlings' day may begin with concentrated feeding, especially by their mother, this is not true at all nests. My records reveal no regular diurnal periodicity of feeding. The rate fluctuates throughout the day, and the number of meals that the nestlings receive in any hour seems to depend chiefly on how hungry they are, which in turn depends upon what they have eaten in the preceding hour. When the two young in Nest 89 were about six days old, the hours of most concentrated feeding were 9:00 to 10:00, when they were fed 21 times, and 16:00 to 17:00,

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when they were fed 19 times. The hours with fewest meals were 7:00 to 8:00, 12:00 to 13:00, and 14:00 to 15:00, in each of which they were fed seven times (Skutch, 1954; Table 8).

Nest sanitation.—Both parents clean the nest, either swallowing the droppings or carrying them off to a distance in their bills. Small droppings are more often eaten, big ones carried away. If a fecal sac breaks in a parent's bill and its pieces fall into the nest, they are usually swallowed. If a dropping falls upon foliage below the nest, a parent flies down and removes it.

Nestling period.—Unless disturbed, young Scarlet-rumped Tanagers leave the nest quite spontaneously, with no parental urging. Of 68 nestlings whose period in the nest I determined, 5 left on the eleventh day after that on which they hatched, 42 on the twelfth day, 18 on the thirteenth day, 2 on the fourteenth day, and 1 on the fifteenth day. Of 42 nestlings whose hour of departure is approximately known, 33 left in the forenoon and 9 after midday. Of those that departed in the morning, 14 are known to have left before 9:00 and 5 between 9:00 and 12:00. From this we may conclude that most of these tanagers permanently sever contact with their nests in the forenoon of the twelfth day after they hatch, and usually early in the morning.

In the most precocious brood that I have watched, the first nestling hatched between 6:25 and 7:15 on 28 May 1944, and the second between 11:30 and 12:50 on the same day. Both spontaneously left the nest between 13:00 and 17:50 on 8 June. The age of the older was then between 11 days 6 hours and 11 days 12 hours; that of the younger between 11 days and 11 days 6 hours. Nestlings less than 12 days old often fly fairly well. One, 11 days and a few hours of age, spontaneously left its nest late in the afternoon and flew from the caña de India shrub in which it hatched to a neighboring cashew tree, where it settled for the night at the very top, about 6 m up, beneath a cluster of leaves but exposed on all sides. Nevertheless, it came safely through the night.

The longest nestling periods, one of 14 days and the only one of 15 days, were those of two young raised in a nest beside a thatched shed where horses and cows took shelter and probably disturbed the parent birds both day and night. The incubation period at this nest was 13 days. Nevertheless, these young tanagers, whose chests and rumps were bright orange, appeared strong and healthy when they flew. In contrast to these nestlings, those raised in the shrub near the kitchen door, where the incubation period was 15 days, left the nest at normal age of 12 days. Here, disturbance was largely confined to the daytime.

From a nest of the nominate race in the Pejivalle Valley of Costa Rica, the nestlings left spontaneously when 11 and 12 days old. From another nest of this race in the Caribbean lowlands of northern Costa Rica, the second nestling, hatched between 12:15 and 16:15 on 22 May 1968, left spontaneously around 6:00 on 2 June, when little more than 10.5 days old. Its nestmate left at 11 days. In Venezuela one Silver-beaked Tanager

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spontaneously abandoned its nest when 11 days old, but another remained until at least 12 days old. In Panama a brood of Crimson-backed Tanagers left at the age of 11 days.

YOUNG AFTER LEAVING THE NEST

After they quit the nest the nearly tailless fledglings, that can fly weakly for several meters, usually disappear quite promptly into the nearest sheltering vegetation—dense shrubbery, a hedge, or a thicket. Here they remain in quiet concealment, while their parents bring them food, their mother usually more than their father. After two or three weeks they emerge, now with well-grown tails, and, flying well, follow their parents about. With quivering wings and shrill calls, they perch on a branch above the feeder, while their parents bring billfuls of banana to them. Soon, becoming bolder, they stand on the board beside the banana while pieces of it are placed in their mouths; and soon they are alternately being fed and feeding themselves. One marked youngster started to feed itself only two weeks after it left the nest, when it was 27 days old.

Full-grown young Scarlet-rumped Tanagers of both sexes resemble adult females, and, like them, show considerable individual variation in the brightness of the chest and rump. Indeed, sometimes a nestling with a fairly bright orange rump and one with a dull yellowish rump lie side by side in a nest. Probably the more brightly colored nestlings and fledglings are males, the duller ones females. The former acquire the scarlet-and-black adult plumage by means of the postjuvenal molt, which begins a few weeks after they leave the nest. In some years young males whose plumage is well flecked with new black feathers have appeared as early as the second week of May, but in other years I have not noticed this change in coloration until June. After many black feathers appear on other parts of the body, scarlet feathers dapple the rump. When the molt of body feathers is well advanced, that of the remiges begins. The rectrices are molted later. By July or early August the most advanced young males are everywhere scarlet and black, except the wing and tail feathers, which are renewed more slowly, but males hatched late, or somehow retarded, may retain juvenal body feathers as late as the second week of October. After this date all the males I have seen wore the full breeding plumage.

Female Scarlet-rumped Tanagers, even when breeding, differ much in coloration. Some have bright orange breasts and rumps, whereas on other individuals these areas are much duller, hardly more orange than I have seen on certain more richly colored females of the nominate race on the Caribbean side of Costa Rica. In view of the fact that the most outstanding difference between the races *passerinii* and *costaricensis* is in the colors of the females' chests and rumps, this variation in the tone of adult females of *costaricensis* is revealing. Probably the colors of these females deepen with age. I have no definite observations on this point; but on several occasions, as when one female wrested a nest from another, the dominant, and therefore

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probably older, individual was the brighter. Another peculiarity of adult female Scarlet-rumped Tanagers is that, on certain individuals, more or less conspicuous flecks or patches of black, on the breast and neck and sometimes also the head, break the uniformity of their paler plumage. I at one time suspected that these slightly black-spotted tanagers were young males belatedly acquiring breeding plumage, but continued observations dispelled this error. They are evidently females with a touch of maleness.

REPLACEMENT NESTS AND SECOND BROODS

These birds lose so many nests to predators that they probably could not maintain their population if they did not try repeatedly to rear a brood. Sometimes they lay again in the pillaged nest. One female started to reline her nest only two days after her eggs disappeared from it; but after two more days her nest also vanished, its materials evidently having been carried off by other building birds, including a Vermilion-crowned Flycatcher (*Myiozetetes similis*) that I saw extracting them. Three females laid replacement sets in their old nests, one about eight days after the loss of eggs that had been incubated for four days; one about 10 days after the disappearance of a four-day-old nestling; and one no more than 16 days after the loss of her first set of eggs. Another female built a new nest in the same small shrub where her first nest was situated, and laid in it seven days after her eggs were taken. Four females made new nests a few meters away from their pillaged structures and laid their first eggs in them 7, 7, 8, and 9 days after the loss of eggs or nestlings. Seven to 10 days appears to be the usual interval between the loss of eggs or nestlings and the laying of the replacement set.

My evidence for second broods after a successful first nesting is scantier. In late May 1942 a pair of tanagers feeding nestlings was followed by a full-grown young bird which clamored for food with nasal, disyllabic cries and relaxed, quivering wings. Half of the food brought by the male parent went to this begging youngster rather than to the nestlings; but its pleas elicited nothing from the female parent, as far as I saw. Again, in early May 1961, an incubating female was followed to the nest by a full-grown juvenile that pleaded for food. After the adult settled on her eggs the young bird continued to hop around her until she left, all the while begging, without receiving either food or a rebuff. Later, the adult female appeared to feed the youngster, which then followed her to the nest, crying for more.

The female that laid in her old nest 10 days after it was ravaged raised a single nestling on this second attempt. A month after the young tanager fledged, this same nest again contained two eggs, apparently laid by the original builder. In mid-July 1942 a female incubated a single egg in a nest which the first brood had left at the end of May. The outcomes of this and the preceding attempt are not known. On 4 May 1961 I found two newly laid eggs in a new nest that had been built on the site of an older one, from which two nestlings had departed just one month earlier.

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This time a single nestling was raised here. Since these tanagers do not defend territories, and the females were not marked, my evidence for second broods is not irrefragable but, taken as a whole, it points to the conclusion that some females nest again about one month after their first brood leaves the nest, when these young have become independent. But, in view of the great loss of nests, I doubt that Scarlet-rumped Tanagers often raise two broods to independence in a single year.

QUESTION OF POLYGAMY

Scarlet-rumped Tanagers, like all other members of their family for which I have information, nearly always nest in monogamous pairs. Even when two nests are close together each female may have her own mate. Thus, in March and early April of 1961, when two females nested only 3 m apart in similar *Thunbergia* shrubs beside our front porch, each had her own partner, which often rested near her nest. We never noticed serious antagonism between them.

Nevertheless, the numerical preponderance of females in the breeding season makes it impossible for all to become regularly paired. Some appear to become attached to males only long enough to have their eggs fertilized. At five nests I failed to find a male in attendance. Two of these nests were so close to my dwelling that if a male had come even occasionally, he would have been noticed. Only one male was present at the nest which a brighter female wrested from a duller one (p. 237). During the contest he was more attentive to the former, which was about to lay, than to the duller female which was already incubating. But, after the brighter female started to incubate in the stolen nest, he went off with the dispossessed one, which probably laid again. The bright female attended her nest alone. Similarly, the single nest with four eggs that I have seen was attended by only one female, although apparently two had laid these eggs. The course of events here was probably similar to that which I had followed in detail in an earlier year: the male accompanied the female which had lost her nest to another female, leaving the intruder alone.

The fact that at every Scarlet-rumped Tanager's nest that I watched the male brought food to the nestlings less frequently than the female did, at some very much less frequently, suggests that he might have fed at two or more nests simultaneously, in the manner of the occasionally polygynous Brewer's Blackbird (*Euphagus cyanocephalus*) (Williams, 1952). However, I have found no evidence of this. The very consistency with which males feed nestlings less frequently than females do casts doubt upon the assumption that they divide their attention among broods. So many nests are lost that it is improbable that nearly all males would have two sets of dependent young at the same time. Males of the related honeycreepers also bring food more seldom than their mates; and among them, too, I have seen no indication that they divide their attention between two nests. The less frequent feeding by males of Scarlet-rumped Tanagers and certain honey-

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creepers appears to be an expression of a slower innate rhythm. They seem not to compensate for their more widely spaced visits to nestlings by bringing them larger meals each time they come. Likewise, after the young leave the nest I have seen them fed more often by their mothers than by their fathers. Nevertheless, the latest fledgling that I have seen, in early December 1957, was fed by a male and not by a female.

I conclude that Scarlet-rumped Tanagers are predominantly monogamous, but that a minority of females, unable to find mates because there are not enough males for all, form irregular attachments with them. In Venezuela I watched two nests of the related Silver-beaked Tanager, situated in the same shrub, without seeing a male show interest in either of them (Skutch, 1968).

NESTING SUCCESS

In Table 7 I have analyzed separately the success of 163 nests of known outcome, at whatever stage they were found, and that of 106 nests, part of the larger sample, found no later than the day the set was completed. Since eggs were often lost soon after they were laid, nests found late in the incubation period, and even more those that already hold nestlings, are a selected group, having escaped disaster for a number of days. Accordingly, we should expect that the total sample, which contains many nests found late, would show higher success than the nests found before or at the date of laying. Surprisingly, my data show the contrary: the success of the nests that I found before or at the beginning of incubation, 44.3 per cent, is substantially higher than that of the larger sample, 38.6 per cent. I attribute this difference to the fact that a larger proportion of the nests found early were situated close to the house, where they seemed to be somewhat safer than those farther afield. Nevertheless, even close beside our house, where we try to protect nests from predators, many are lost to them.

TABLE 7
Nesting Success of Song Tanagers

All nests of known outcome	163
Nests successful (at least 1 young fledged)	63
Nests failed completely	100
Per cent of nests successful	38.6
No. of above nests found not later than beginning of incubation	106
Nests successful (at least 1 young fledged)	47
Nests failed completely	59
Per cent of nests successful	44.3
Eggs laid in 106 nests	207
Eggs hatched	121
Per cent of 207 eggs hatched	58.4
Young fledged from these eggs	86
Per cent of 207 eggs producing fledglings	41.5
Per cent of 121 hatchlings fledged	71.1

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The chief known cause of loss of eggs and nestlings is predation by snakes and squirrels. Although I earlier told of the Scarlet-rumped Tanagers' boldness in attacking snakes, they seem rarely able to save eggs or nestlings from them. We do not withhold succor in order to learn how successful the parents' defense would be; but on several occasions, alerted by the birds' cries of distress, we have found the serpent in the act of swallowing the eggs, or with an egg or two already in its body. On one occasion, as already described, a very slender snake seized the defending parent.

Likewise, these tanagers are unable to protect their nests from Cinnamon-bellied Squirrels (*Sciurus granatensis*). In my early years at Los Cusingos, Chestnut-mandibled Toucans (*Ramphastos swainsonii*) and Fiery-billed Araçaris (*Pteroglossus frantzii*) periodically raided nests in the garden, including, no doubt, those of Scarlet-rumped Tanagers, undeterred by even the boldest of distressed parents. With the destruction of most of the rain forest in the valley, the big toucans disappeared long ago. The more agile araçaris remain but have become less numerous. Nocturnal predators, including opossums, smaller marsupials, other mammals, and snakes doubtless destroy many nests but have not been seen in the act.

On the whole, the tanagers appear to do somewhat better now than when I first came here and the region was much wilder. In 1944, when I tried to find all the nests of tanagers and other birds in 3.75 acres (1.5 hectares) of shady dooryard and pasture around my house, I discovered, between March and July, 23 nests of these tanagers, counting only those in which at least one egg was laid. Of these, only five or six (22 or 26 per cent) were successful, each yielding one or two fledglings. As far as I could learn, these 23 nests were built by only five or six females, which tried again and again until they reared a brood, or the nesting season ended.

CAN SCARLET-RUMPED TANAGERS RAISE MORE THAN TWO YOUNG?

For the last three decades ornithologists have been asking whether birds, especially in the tropics, raise as many young as they can adequately attend. As we have seen, with rare exceptions, Scarlet-rumped Tanagers lay no more than two eggs. Of the five nests with a larger number that I have seen, one contained three eggs which were certainly laid by two females, and another had four eggs most probably laid by two females. In the first of these nests only one egg hatched; in the second the whole set was lost, apparently by predation. This leaves three sets of three eggs, evidently laid by the same female in the same small area in 1946, 1947, and 1949. In each of these three nests all three eggs hatched. In the first two of these years I had not become interested in the question of the regulation of brood size, but I watched each of these nests (Table 6, Nests 124 and 135) long enough to assure myself that a male helped to feed the nestlings.

By 1949 my interest in this question had been aroused by Lack's (1947-1948) generalization that birds rear as many young as they can adequately nourish, which did not appear to me to be true of certain tropical birds. On two

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days I spent 12 hours, which together covered all parts of a day, simultaneously watching a nest with three nestlings and a nearby nest with the usual brood of two. The results are given in Table 6, Nests 167 and 169. Here it will be seen that the two nestlings seven and eight days old were fed by both parents at the average rate of 7.2 times per nestling per hour, while the three nestlings 10 and 11 days old were fed by both parents at the rate of 5.8 times per nestling per hour. In the first five hours of the morning, however, the two broods were fed at nearly the same rates: at Nest 169, 7.9 times, and at Nest 167, 7.7 times per nestling per hour. At the same age, during the same hours of the morning, three 11-day-old nestlings in Nest 124 were fed at the rate of 5.7 times per nestling per hour. This may be compared with the rate recorded at Nest 89, where two 11-day-old nestlings were fed at the rate of 5.9 times per nestling per hour, but in the afternoon rather than the forenoon. The observations at Nest 151 (Table 6 and p. 252) also demonstrated that Scarlet-rumped Tanagers are quite capable of increasing their rate of feeding to satisfy an abnormally large brood.

The female that laid three eggs in three different years (Nests 124, 135, and 167) reared, with her mate's help, three nestlings in the first year, two in the second, and three in the third. All left the nest at the usual age and appeared vigorous. Although most nestlings vanish into dense vegetation soon after they quit the nest, I was able to find those of the last of these broods four days after their departure. All three were perching close together in a shrub. They flew well.

I have only one record of a brood of two in a nest without an attendant male. Here the solitary female succeeded in raising both nestlings, at least until they fledged. Although I did not weigh any of these nestlings, it is possible that trios, or two with a single attendant, fledged weighing somewhat less than those in normal broods of two. However, this need not have affected their subsequent viability, for lighter fledglings may survive as well as heavier fledglings, as demonstrated by Snow (1958) for the Blackbird (*Turdus merula*), and Woolfenden (1978) for the Florida Scrub Jay (*Aphelocoma coerulescens*). I conclude that Scarlet-rumped Tanagers are capable of rearing broods larger than their usual two, but they do not because, even with their small families, they remain abundant, and selection pressure has not been strong enough to increase the number of eggs that the females lay, or the males' diligence in feeding their offspring.

SUMMARY

This chapter deals chiefly with the western, or Pacific, race of the Scarlet-rumped Tanager, which has been called the Song Tanager because males sing more profusely than most other tanagers. Females differ from those of the eastern race in their richer colors.

These tanagers do not defend territories. At all seasons they straggle through shady pastures and dooryards, plantations, and thickets in loose

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flocks of about a dozen individuals, among which females are more numerous than males. They enter the more open parts of rain forest to forage, but have not been found nesting in woodland. They are exceptionally nervous, suspicious, excitable birds.

They eat a great variety of fruits and arillate seeds, vary their diet with insects and spiders, and occasionally sip nectar from flowers. Rarely they eat a lizard or baby mouse.

Two diseases are described.

These tanagers are generally peaceable but, contrary to an earlier report, males do fight, although rarely. One female wrested a nest from another without fighting.

When a snake appears they sound the alarm, and they continue to pursue and harass the reptile as long as it remains in the vicinity of their nests. Although bold in attacking snakes, they are held aloof by the intimidatory displays of edible insects such as mantises and locusts. They mob big, bedraggled moths and even strange inanimate objects.

The nest site may be chosen by both sexes, or by either sex alone. The substantial open cup is placed in a shrub, densely foliated tree, or vine tangle, at heights of from 36 cm to 6.4 m, but more than half are from 1.2 to 2.5 m up. The female, often escorted but never helped by her mate, usually builds the nest in three to six days, although the season's earliest nests may take twice as long. Most are widely spaced, but occasionally two active nests are situated only a meter or even centimeters apart.

In the Valley of El General most eggs are laid in March, April, and May, fewer in June, and very few until September or even later. With very few exceptions two eggs are laid, around sunrise on consecutive days. The rare sets of three or four are sometimes the product of two females; but three sets of three eggs were apparently laid by the same female in successive years. The first egg is laid one to three nights, rarely more, after the nest is finished.

Rarely the female lays her second egg in the nest from which the first was promptly lost, but more often she abandons the pillaged nest.

Only the female incubates. Often she sleeps on her single egg before laying the second. Her time on the nest increases gradually, reaching a constancy of 71 to 75 per cent, rarely more. Nuptial feeding has not been observed; but, from time to time, a male brings food to the nest, anticipating the nestlings.

Eggs may hatch in as little as 12 full days, but the average length of the incubation period is 12-1/4 days. Shells are promptly eaten by the female.

Nestlings are brooded by the female and fed by both parents with insects and fruits. Males may begin to bring food before they see a nestling, sometimes as little as 38 minutes after the first hatches, but occasionally they delay a full day to begin feeding. Rarely a male brings food almost as frequently as his mate does, but many males feed much more seldom. Rates of five

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to eight meals per nestling per hour are usual through most of the nestling period.

Most nestlings leave the nest spontaneously in the forenoon of the twelfth day after they hatch. A minority leave on the eleventh or thirteenth day, and very few at a greater age. On leaving the nest they can fly weakly for several meters; and they are promptly led into dense vegetation, where they remain hidden for two or three weeks. Two weeks after leaving the nest they begin to feed themselves.

Males fledge in a plumage like that of the female. They acquire the black-and-scarlet adult plumage by the postjuvenal molt. By August most young males can be distinguished from older ones only by their juvenal remiges and rectrices, which are replaced more tardily.

From seven to 10 days after the loss of eggs or nestlings, females may lay again, sometimes in the old nest, often in a new one nearby. Second broods are sometimes started about one month after the first brood leaves the nest.

Most Scarlet-rumped Tanagers nest in monogamous pairs. Since adult females are more numerous than adult males, a few form irregular attachments and attend their nests without a male's help.

Of 163 nests of known outcome, found at all stages, 38.6 per cent yielded at least one fledgling. Of 106 of these nests, found not later than the beginning of incubation, 44.3 per cent were successful. The higher success of the latter is attributed to the fact that they tended to be nearer the house. The chief known predators were snakes and squirrels.

Although they regularly lay only two eggs, Scarlet-rumped Tanagers are able to raise three nestlings.

GRAY-HEADED TANAGER

Eucometis penicillata

Bright olive-green upper plumage and clear saffron-yellow underparts make the 17 cm Gray-headed Tanager easy to recognize in the lower levels of humid forests, where it seems to feel most at ease. From the woodland depths it often ventures forth into neighboring shady clearings and plantations, to forage and, even more, to nest; but, when its business there is done, or when it feels endangered, it hurries back to the sheltering woods. Even when nesting in a clearing, it regularly returns to the forest to forage. Constantly twitching its wings and tail, avoiding observation by man while it repeats a subdued *chip*, it appears to be an extremely nervous bird. Throughout the year it lives in pairs which, after the nesting season, are accompanied for some weeks by full-grown young, able to nourish themselves. It is one of the best songsters in the tanager family that I know. The male's sweetly appealing, flowing song sometimes sounds like *Whichis whichis*

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whicheery whichis whichú, but he has many variations. Sometimes he ascends as high as mid-levels of the forest and continues for minutes together to pour forth his dulcet notes.

This distinctive tanager, the only species of *Eucometis*, ranges from southeastern Mexico to Bolivia, southern Brazil, and northeastern Argentina. In the north it has been found only at low altitudes, up to 250 m in Guatemala (Land, 1970) and 500 m in Honduras (Monroe, 1968). In my earlier account of the tanager (1954) I gave its altitudinal range on the Pacific slope of southern Costa Rica as from the lowlands up to at least 1,050 m. I have since found it ranging as high as 1,200 m in extreme southern Costa Rica and, across the border in Panama, it has been seen as high as 1,650 m (Ridgely, 1976). In Venezuela it ascends to 1,200 m (de Schauensee and Phelps, 1978).

FOOD

The Gray-headed Tanager is the only member of its family in Central America that might be called a "professional" ant follower. When a man comes into view of the swarming army ants, it tends to melt away into the underwood and is more difficult to watch than many of its associates in the mixed flocks that accompany the ants, such as the confident Bicolored Antbirds (*Gymnopithys leucaspis*). It readily yields to bolder birds. In Venezuela I twice saw a Barred Antshrike (*Thamnophilus doliatus*), not a regular ant follower, drive a slightly bigger Gray-headed Tanager from the insect it was about to seize. When I approached nearer both the tanager and the antshrike vanished into a thicket. The latter soon returned to forage in my presence, but not the timid tanager. I have rarely seen more than one pair of these tanagers, frequently with full-grown young, with a swarm of ants. When two pairs are present one tanager often chases another. Like other ant followers, Gray-headed Tanagers catch the insects and other small fugitives from the hexapod legion, rather than the ants themselves.

On the morning of 5 February 1964, four domestic hens scratched industriously just within the forest's edge beside our garden. With them was a pair of Gray-headed Tanagers, profiting by their industry. The tanagers perched from a few centimeters to a meter or so above the ground, above or near the hens, nervously twitching their wings and tails, as is their manner, and from time to time uttering low, dry notes. Again and again a tanager alighted on the ground where a hen had just scratched and moved on, evidently to catch an insect that the chicken had uncovered but missed. The tanagers often flew from perch to perch above the scratching hens, possibly to catch flying insects that the hens had stirred up. When the party of scratchers was augmented by a cockerel and several more hens, the tanagers stayed with it. For three quarters of an hour after I found them, the tanagers continued to forage with the chickens, all in the same small area. When the chickens moved about 10 meters along the forest's edge, their small attendants followed, but when the domestic fowl walked

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out into the open pasture, the tanagers flew back into the forest.

When I entered this forest on the morning of 28 September 1976, two young Gray-headed Tanagers, still with olive crowns, remained in the undergrowth beside the path, instead of flying off, as these shy tanagers usually do. As I walked along the path they followed in a parallel course through the trees. When I paused again, after walking a hundred meters, these same two birds were nearby, voicing low notes and seeming to be watching me. Suspecting that they were following me for the insects set in motion by my passage, I left the path to move through the undergrowth, where I would stir up more insects. But my unavoidably noisy passage, through bushes, vines, and fallen branches put the tanagers to flight, and I saw no more of them. I could not induce these timid birds to follow me for the food I made available, as Bicolored Antbirds have repeatedly done (Skutch, 1969, 1980). The behavior of these two young tanagers, and that of the pair that foraged with hens, suggests that, when they cannot find a swarm of hunting ants, Gray-headed Tanagers seek large terrestrial birds, and even mammals, as purveyors of insects.

As one expects of ant followers, Gray-headed Tanagers appear to depend more upon insects and less upon fruits for their food than do most other members of the family. My feeder, 50 meters from the forest where Gray-headed Tanagers dwell, had been in operation for more than 20 years, and had attracted 27 other avian species, before, in January 1964, I saw Gray-headed Tanagers come to eat the bananas displayed there. This was a few weeks before I watched the pair forage with the hens. Evidently difficulty in finding army ants, or a scarcity of other foods, forced these tanagers to seek new sources of nourishment. Since that date their attendance at the feeder has been most sporadic; many months may pass without their appearance, even when they are nesting in the garden. One morning in April I watched a Gray-headed Tanager go to the board, take a billful of banana, and carry it to a neighboring orange tree, where his mate received it with quivering wings. Then both flew back to the forest. In August of a later year a pair came with young as large as themselves. Their heads and necks were only slightly darker than their greenish olive backs, and they kept up a continuous rapid peeping. On the board they fed themselves, taking very small bits of banana, and their parents still fed them.

I have only rarely found Gray-headed Tanagers at fruiting trees frequented by other species of tanagers and a great variety of other birds. I have seen them eat the berries of *Miconia trinervia*, and pluck a seed of *Protium* enclosed in its soft, white aril, carrying it off whole, probably to peck off fragments in some quiet retreat, since it was too big to be swallowed entire.

NESTS

In southern Central America, Gray-headed Tanagers, which have long been paired, begin to nest in March. In old forest or tall second-growth woods, the nest is often placed in the crown of a small palm that bristles

with long, sharp, black spines. Of the seven nests that I have found in woodland, six were in such palms, the seventh in the vertical fork of a small sapling beside a dry watercourse. Most of the 31 nests that I have recorded were not in forest but in clearings in forested country. Nine were in coffee bushes in small plantations; nine in young orange trees; one in a privet hedge; one in a *Piper* shrub; one between the stout, clustered, upright stalks of a tussock of Job's-tears, a coarse grass growing in a neglected banana plantation. Two were among vines. In height, 31 nests ranged from 63 cm to 3 m above the ground; but the great majority, 23 nests, were from 1.5 to 2.1 m up. Six were under 1.5 m, and only two above 2.1 m. The highest nest was in a bush that leaned over the edge of a cliff, 3 m above the ground directly beneath it, but not so far above the top of the cliff. The next highest was 2.5 m up, among hanging vines draped over a small tree in tall second-growth woods.

At four nests that I watched during construction, both sexes brought material and sat in the nest to shape it. The two often came and went independently, instead of flying back and forth together, as species of *Tangara* do. When one, arriving with material, found the other in the nest, it often passed its contribution to its partner, which then placed it in the structure. However, some of the builders were reluctant to relinquish what they had brought, and so impatient to occupy the nest that they sat or stood upon the partner that was there before them. The sudden departure of the bird below would make the newcomer fly off, too, but it promptly returned to deposit its contribution. While building the tanagers were noisy, calling much, the males singing sweetly even while holding a billful of material or sitting in the nest to shape it. At a fifth nest, watched only during the last day of building, all the work appeared to be done by the female, which brought material 17 times in the hour from 6:20 to 7:20, was absent from 7:20 to 8:00, and came six times from 8:00 to 8:30. Although her mate sometimes accompanied her, he neither sang nor built. Some pairs finished their nests in 2 or 3 days, others took 5 or 6 days.

The finished nest is a thin-walled, shallow cup, often so slightly built that the eggs are visible through the bottom. Some nests are composed almost wholly of brown or blackish rootlets and fungal filaments that resemble horsehair. One was made of fibrous rootlets, loosely matted and lined with long, brown, threadlike pistillate inflorescences of the small tree *Myriocarpa yzabalensis*, much used by building birds which apparently disperse the minute seeds while carrying the material to their nests. Another was made of blackish rootlets, mixed with many small, delicate living ferns, including two kinds of filmy ferns and *Rhipidopteris peltata*. The nest in the clump of Job's-tears was as unusual in its structure as in its site, being loosely made with coarse petioles, lengths of slender vines, dry flower stalks, and a few dry fern pinnae. Many of the petioles projected untidily from the walls. The lining was of slender rachises of acacia leaves and some black fungal strands. A typical nest was 10 cm in over-all diameter by 6 cm high. The cavity was 8.5 by 6.5 cm in diameter and 4.5 cm deep.

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In wet weather the hairlike fungal rhizomorphs that Gray-headed Tanagers build into their nests may continue to grow. A nest in an orange tree, which was used for one brood the first year and two broods in the following year, had become very frail. At the end of May in the second year I noticed that the brown rhizomorphs had sent out thin, straight branches that stood up vertically all around the nest. Most were only a few centimeters high, but a few had climbed upward as much as 60 cm, attaching themselves to the trunk, branches, and leaves of the orange tree. Probably the building tanagers had gathered such strands from similar situations.

EGGS

In one nest, which was exceptionally frail, the first egg was laid only 3 days after building started. At three nests the interval between the start of building and the appearance of the first egg was 5 or 6 days. At two nests this interval was 8 or 9 days. One of these nests was begun on 11 July 1949 and seemed finished by 15 July, but the first egg was not laid until 20 July. This late nest was for a second brood.

The two or, rarely, three eggs are laid early in the mornings of consecutive days. Eleven eggs were laid before 7:00, at least seven of them before 6:45. At least three eggs were laid between 6:00 and 7:00. A Gray-headed Tanager that lost her first egg the day it was laid deposited her second egg in the empty nest on the following morning; but this, too, promptly vanished. I have also known Scarlet-rumped Tanagers (*Ramphocelus passerinii*), Silver-throated Tanagers (*Tangara icterocephala*), Buff-rumped Warblers (*Basileuterus fulvicauda*), and Lesser Elaenias (*Elaenia chiriquensis*) to lay their second egg in the nest from which the first was lost.

Twenty-five nests of the Gray-headed Tanager contained 2 eggs or nestlings, and four nests held 3. The eggs are pale blue-gray, heavily mottled with dark shades of brown, which on the thicker end almost mask the ground color. On most eggs the brown blotches are rather crowded over the whole surface, but on some they are few and scattered toward the sharper end. Sometimes the brown marks take the form of scrawls, and some eggs bear a few flecks of black. The measurements of 12 eggs average 24.2 by 17.3 mm. Those showing the four extremes measured 25.4 by 18.3, 22.6 by 17.5, and 25.0 by 16.7 mm.

In the Valley of El General 30 sets of eggs were laid as follows: March, 2; April, 5; May, 12; June, 8; July, 3.

INCUBATION

As in all other tanagers that I have studied, only the female incubates. One female filled her morning with three sessions, lasting 66, 97, and 66 minutes, and two intervening recesses of 25 and 66 minutes. She incubated with a constancy of 62.6 per cent. Another female, also watched for six morning hours, took four sessions of 48, 45, 53, and 97 minutes, with recesses of 20, 20, 22, and 55 minutes. She covered her eggs for 67.5

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per cent of the forenoon. The mate of this second female was more songful and attentive than that of the first female, coming to call her from the nest throughout the morning, and accompanying her on at least three of her four returns to her nest in a coffee bush. The first of these nests was about 80 m, the second 125 m, from the forest to which the tanagers flew to forage. The female tanager, a bird of deep forest, panted in the late morning, even in the light shade of the coffee grove.

Early in May 1959 I found a Gray-headed Tanager's nest 1 m up in a privet hedge. Although I visited it daily to learn whether an egg would be laid, I never saw one. Nevertheless, a tanager sometimes flew from the empty nest as I approached. Puzzled by this behavior, I went in the night and found the bird sleeping in the nest. Setting up my blind I watched through most of a morning. In five hours I timed three sessions of 25, 70, and 61 minutes' duration, and three absences of 29, 48, and 52 minutes. The tanager was sitting in an eggless nest in the pattern of a bird normally incubating, but with the somewhat lower constancy of 54.7 per cent. She had a mate that accompanied her to the forest across the pasture. For at least two weeks—long enough to hatch eggs if she had them—this strange bird continued to sit in her empty nest by day and to sleep in it at night. Possibly she had laid eggs that I failed to see because they were taken by some predator soon after laying, as not infrequently happens. Except broody domestic hens, I have never known another bird to "incubate" without eggs, but others have reported similar cases. In New Zealand the Takahe (*Notornis mantelli*) may sit, as though incubating, in eggless nests. One pair took turns doing so for seven or eight weeks (Williams, 1960).

In seven nests the incubation period was 14 days; in one it was prolonged to 16 days. The Gray-headed Tanager's eggs take two days longer to hatch than the slightly smaller eggs of the Scarlet-rumped Tanager. Doubtless because she flies farther to forage with army ants, the female Gray-headed Tanager's absences from the nest are very much longer than those of the Scarlet-rumped Tanager. In the thin, poorly insulated nest, her eggs lose much heat, thereby retarding embryonic development. A thin nest dries more quickly than one that is well padded, but the price that it pays, in the form of lengthened incubation with longer exposure to predation, may be high. A similar situation is found in hummingbirds, among which eggs in the thin, fibrous nests of certain hermits (*Threnetes*, *Glaucis*) take two or three days longer to hatch than do eggs in nests thickly lined with downy materials.

NESTLINGS

The hatchlings bear loose gray down, too sparse to conceal their dark skins. They have tightly closed eyes, and the interior of their mouths is red. They are fed by both parents, largely with insects, which at nests in clearings may be brought from the forest a hundred meters away. Two nestlings 10 days old were fed 32 times in four hours, or at the rate of

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four feedings per nestling per hour. One female, which while incubating always flew from her nest while I was still distant, remained covering newly hatched nestlings until I approached within two meters. Then she dropped to the ground and hopped haltingly away, as though her legs were crippled, but without beating her wings in a typical "injury feigning" display. Nevertheless, this was the best distraction display that I have seen any member of the tanager family give. She vanished amid the bushes, but soon returned to perch near me, complaining with low notes, while I examined her nestlings—an exceptional display of parental devotion by this very shy bird. Another parent Gray-headed Tanager dropped to the ground beside me when its feathered young fluttered from the nest, but it did not simulate injury.

One nestling had two large swellings on its head, caused by the fly larvae known as *tórsalos*, which appeared not to have seriously affected its development. The nestlings' feathers begin to unsheathe when they are seven days old, and at 10 days they are fairly well clothed with plumage, which is olive dorsally and pale yellow, heavily clouded with olive, on their ventral surface. They may be brooded on their last night in the nest. Seven nestlings left six nests when 11 days old; five left five nests as 12 days of age. Often one member of a brood leaves when 12 days old and its sibling when 11 days old. Two nestlings abandoned their nest on the tenth day after hatching. I was not convinced that they had left their nest alive until I found one of them in the thicket beside the coffee plantation where they hatched. It was perching 3 m up in a bush and receiving food that its parents brought from the distant forest. A 12-day-old fledgling flew rapidly at least 15 m, hardly losing altitude. Although often raised in a clearing, the young are soon led into the forest.

LATER BROODS

Two or three times I have known Gray-headed Tanagers to undertake a second brood, which in one instance was successful. The two fledglings of the first brood left the nest on 15 June. On 24 June the first egg was laid in a new nest, 35 m from the first, and here two more young were reared. They left the nest on 21 July. In the following year the same pair raised one young, which left the nest on 26 June. On 20 July the female laid the first egg of her second brood in a new nest 10 m from the first. This second brood failed. A probable instance of two broods successfully reared by the same pair was found in 1979, when two young of the first brood left a nest 2 m up in an orange tree on 1 June, and about 15 June two eggs were laid in an exactly similar site 63 m away.

Replacement nests are not rare. In 1977 a pair that built in young orange trees in our riverside pasture tried three times before they succeeded in raising nestlings. The female laid her first set of eggs on 14 and 15 May, and hatched them on 29 May; but by 7 June her nest was empty. On 15 and 16 June she laid, in a new nest about 30 m from the first, her

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second set of eggs, which had vanished by 24 June. Then, about 3 July, she laid two more eggs in the first nest, from which two fledglings departed on 29 July. The intervals between the loss of a nest and the resumption of laying were about eight and nine days. In the following year what I believe to have been this same pair lost three eggs from a small orange tree on 8 April, and on 28 April the female laid the first egg of another set of three in another small orange tree, about 100 m from the first. The separation of the first and second nests was great, but the rarity of three-egg sets makes it probable that they were laid by the same female.

NESTING SUCCESS

Of 24 nests of known outcome, found at all stages, nine yielded at least one fledgling, giving a gross nesting success of 37.5 per cent. In 17 of these nests, found before incubation began, 35 eggs were laid, 17 eggs hatched, and 9 young fledged from 5 nests. Forty-nine per cent of the eggs hatched; 53 per cent of the hatchlings lived to fledge; 25.7 per cent of the eggs produced a fledgling; and 29.4 per cent of the nests yielded one or two fledglings. The chief cause of loss was predation. Of the larger sample, one nest was deserted for unknown reasons; two eggs survived but failed to hatch, evidently because they were infertile; and one nest was covered with shredded particles of the lining, leaving two of the three eggs intact. This was probably the work of a mouse.

SUMMARY

From the humid forests where it lives in pairs throughout the year, the Gray-headed Tanager enters adjacent clearings to forage and to nest. For a tanager, it has an exceptionally beautiful song.

A "professional" ant follower, it may forage above scratching chickens when it cannot find army ants. It is seen at feeders, where bananas are offered, and at fruiting trees more seldom than most other tanagers.

In the Valley of El General it breeds from March to July, with a peak in May. Most nests are 1.5 to 2.1 m up, with extremes of 63 cm and 3 m. Often placed in spiny palms in woodland, in clearings they are built in orange trees, coffee shrubs, tussocks of coarse grass, or hedges. Usually both sexes build the thin-walled cups in three to six days.

Two, rarely three, eggs are laid early in the morning on consecutive days.

Only the female incubates, taking long sessions and recesses, and sitting with a constancy of 60 to 70 per cent. One female "incubated" in an eggless nest for at least two weeks. The incubation period is 14 days, rarely longer.

Both parents feed the nestlings, largely with insects. The only distraction display I have seen among tanagers was given by a Gray-headed Tanager, but even in this species such displays are rudimentary and rare.

The nestling period is 11 or 12 days, rarely 10 days. Although often raised in a clearing, fledglings are soon led into the woods.

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Second broods are sometimes raised; and, after two failures, a pair may nest a third time. The first egg in a replacement nest is sometimes laid eight or nine days after the loss of the first nest.

Of 24 nests found at all stages, 37.5 per cent yielded at least one fledgling. In 17 nests found before incubation began, 25.7 per cent of 35 eggs produced a fledgling.

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